Neuropsychological Studies of Phantom Sensations and Corporeal Awareness in Healthy Subjects

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Abstract

The present thesis investigated several aspects of corporeal awareness in healthy volunteers against the background of what is known about phantom sensations in amputees. Several techniques were applied to achieve a better understanding of how body awareness in healthy subjects may be manipulated. Specifically, this thesis examined the following questions: (1) whether individual differences in cognitive processing and bodily experience may have an impact on the perception of experimentally induced bodily illusions in healthy subjects, (2) whether there might be mechanisms common to the dual experience of a single stimulus in healthy volunteers (*Mitempfindung*) and in amputees (referred sensations), (3) whether the effects of cross-modal interference between vision and touch can be found in a patient without conscious touch experiences, and (4) whether the perception of a cross-modal illusion (the Rubber Hand Illusion) can be elicited in a patient who, due to amputation, does not have a hand.

The studies presented in this thesis revealed that (1) vibration induced phantom sensations are at least partly mediated by cognitive processes and by everyday experiences of fleeting bodily illusions ("perceptual aberrations"), (2) there are a number of conceptual similarities between *Mitempfindung* and synesthesia, leaving the question if there are similarities between Mitempfindung and referred sensations open to debate, and (3) it is possible to capture unconscious touch by vision, which might be linked to the phenomenon of "numbsense", denoting a residual tactile sensitivity in an otherwise deafferented patient. The fourth question could not be answered due to our failure to find a subject fulfilling all required inclusion criteria. The study is, however, outlined in enough detail, so that testing can easily be accomplished should an appropriate participant be found.

On the one hand, the findings presented here show how easily corporeal awareness can be manipulated in normally limbed individuals. On the other hand, they demonstrate a considerable variation in the resistance towards bodily illusions among healthy subjects.

In the long run, the results discussed here might help to better explain the genesis of phantom sensations in amputees and the contribution of vision to corporeal awareness.

Zusammenfassung

In der vorliegenden Dissertation wurden verschiedene Aspekte der Körperwahrnehmung gesunder Versuchspersonen untersucht. Diese Untersuchungen war eingebettet in den grösseren Kontext der Phantomempfindungen, die von Amputations-Patienten bekannt sind. Dabei wurden verschiedene Techniken angewendet, um ein besseres Verständnis der Körperwahrnehmung gesunder Versuchspersonen zu erhalten. Insbesondere beschäftigt sich diese Dissertation mit folgenden Fragen: (1) Welchen Einfluss haben kognitive Verarbeitungsstrategien auf die Wahrnehmung experimentell induzierter Körperillusionen bei gesunden Versuchspersonen? (2) Basieren die von gesunden Personen bekannten Mitempfindungen und die von Amputierten bekannten *referred sensations* auf ähnlichen Mechanismen? (3) Ist es möglich, in einer Patientin ohne bewusste Berührungsempfindungen eine Interferenzen zwischen Sehen und Fühlen hervorzurufen? (4) Kann die sogenannte Gummihand-Illusion, eine multimodale Illusion, die aus eine Konflikt zwischen Sehen und Fühlen resultiert, in einem handamputierten Patienten evoziert werden?

Die hier vorgestellten Studien zeigen, (1) dass vibrations-induzierte Illusionen zumindest teilweise von kognitiven Prozessen und dem Erleben vorübergehender Veränderungen der Körpererfahrung im alltäglichen Leben ("perceptual aberrations") vermittelt werden; (2) dass es eine Reihe konzeptueller Gemeinsamkeiten zwischen Mitempfindung und Synästhesie gibt, (3) dass es möglich ist, Berührungsempfindungen, die nicht bewusst wahrgenommen werden, nichtsdestotrotz durch visuelle Wahrnehmungen zu beeinflussen. Ein Effekt, der mit residueller taktiler Wahrnehmung bei ansonsten kompletter Deafferenzierung ("*numbsense*") in Verbindung gebracht wird. Die vierte Frage konnte nicht beantwortet werden, da es nicht gelang, eine Person zu finden, die alle nötigen Einschlusskriterien erfüllte. Die Studie wird nichtsdestotrotz detailliert als konzeptueller Entwurf vorgestellt und kann jederzeit durchgeführt werden, sollte sich eine geeignete Versuchsperson finden.

Die berichteten Resultate zeigen einerseits, wie einfach die Körperwahrnehmung gesunder Versuchspersonen manipuliert werden kann. Andererseits zeigen sie, wie verschieden die Resistenz gegen körperliche Illusionen bei gesunden Versuchspersonen ist.

Es ist zu hoffen, dass die vorgestellten Resultate zumindest indirekt helfen, das Entstehen von Phantomempfindungen bei Amputierten und den Einfluss des Sehens auf die Körperwahrnehmung besser zu verstehen.

Preface

In 1797 the famous Lord Nelson lost his right arm in an unsuccessful attack on a treasure ship at Santa Cruz de Tenerife (Fig. 0.1). Afterwards, he experienced excruciating pain in the arm he had lost and took this experience as proof that there is life after death. He argued that if an arm could survive physical annihilation, the soul surely should do so as well (Riddoch, 1941). Not until about 80 years later, the phenomenon Nelson had experienced was given the name it still has today: in the middle of the 19th century American neurologist Silas Weir Mitchell coined the term "phantom limb". Despite the long history of medical interest in phantom sensations, the phenomenon is still rather enigmatic even today. Some researchers suggest that phantoms remained a mystery for much of medical history because the experience of body parts which no longer exist, contradicted what was known about how feedback from the physical body was necessary for the experience of this body (Halligan, 2002).

Fig. 0.1: John Hoppner:
Admiral Lord Nelson.

Today, our knowledge about phantom sensations is ever growing but still fragmentary. To add another piece to the puzzle, the present thesis is part of the project "Phantom sensations after deafferentation/deefferentation and their simulation in healthy subjects: visual-sensorimotor interactions", funded by the Swiss National Science Foundation. The project was split into three parts:

Marion Funk examined motor imagery and phantom sensations in patients missing limbs from birth (congenital limb aplasia) and developmental aspects of body representations.

Sabina Hotz Boendermaker focused on movement observation and phantom limb experiences in patients with spinal cord injuries (paraplegic patients).

The goal of my thesis was to investigate body perception in healthy volunteers to help understand the phenomenon of phantom sensations. Chapter 1 of this thesis will give a short introduction to phantom sensations in clinical populations. Chapter 2 introduces my main topic: body perception in healthy volunteers. Different components of the central representation of the body are described and the methods used to manipulate bodily experiences are discussed. Chapter 3 contains my own experimental results, describing the studies I conducted during the course of my doctoral thesis. A general discussion of the results within the framework of currently proposed models is given in Chapter 4. Finally, a comprehensive reference list is given at the end, and the materials used are found in the Appendix.

Chapter 1

Phantom Sensations in Clinical Populations

This chapter provides an introduction to the topic of phantom sensations as they are found in clinical populations.

Definition

Phantoms are "the report of the awareness of a non-existent or deafferent bodily part in a mentally competent individual“ (Weinstein, 1969, p. 79). That means that a body part that no longer exists (as in amputees) or has never existed (as in patients missing limbs from birth) is nevertheless being experienced as part of the own body by the individual.

According to Melzack (1990), several features distinguish phantom limbs from other forms of disorders of the body: they have the quality of unshakable reality for the amputee, they can be comprised of a wide range of sensations and - last but not least - they are experienced as an integral part of the self.

Phantom sensations arise most often after the deafferentation of a body part and may occur in amputees, patients with spinal cord injury and persons with congenital limb aplasia. After lesions of the right parietal lobe the experience of extra body parts, "supernumerary phantoms", has been described.

The most well known phantom sensations are amputation phantoms after surgical removal of a limb, which may also occur after removal of breasts, nose or internal organs. Phantom limbs usually take the shape of the amputated limb, which means that malformations may be carried over into the phantom (Halligan, 2002).

According to Ramachandran & Hirstein (1998) up to 98% of all adult amputees will experience phantom sensations soon after the amputation. This initial experience will persist in 30% of the cases. Phantom sensations include sensations of complete or partial limbs, as well as sensations of (in)voluntary movement, warmth, cold or pain. Up to 70% of phantom sensations may include the sensation of pain (Halligan, 2002). Due to the intractable nature of phantom pain, this leads to permanent disability in more than 40% of the patients (Pezzini et al., 2000).

Referred Sensations

Referred sensations are found in some amputees with phantom sensations and denote the referral of stimuli delivered to the body onto the phantom, that is, a suprathreshold stimulus is felt not only at the stimulation site but also at another site of the body. The referral of stimuli delivered to the stump onto the phantom has been know since at least 1872 (Mitchell, 1872). Not until much later it was discovered that the stimuli eliciting referred sensations can form actual topographical maps on the stump near the amputation site. That means, it is possible to draw maps of, for instance, finger representations onto the stump, in which the fingers are represented in an orderly fashion. Moreover, these topographical maps are found not only on body parts that used to be adjacent to the amputated limb on the body surface, but also on body parts that are adjacent to the amputated limbs in the body representation that is found in the brain (the so called homunculus, see Fig. 1.1, Ramachandran and Hirstein, 1998). The homunculus reveals that the somatosensory areas of the face and the hand lie adjacent to each other on the surface of the brain. This explains why topographical maps of fingers may also be drawn onto the face of hand amputees (see Fig. 1.2).

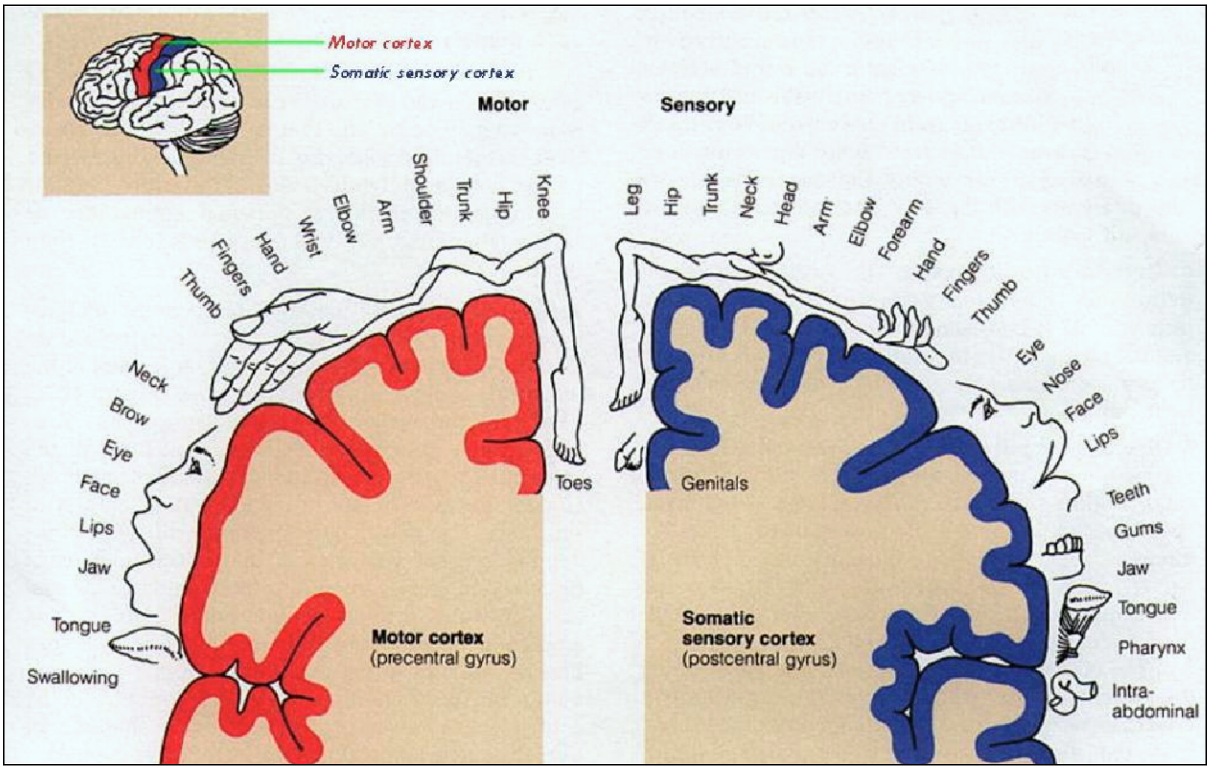


Fig. 1.1: Human Body Representation on Primary Motor (MI) and Somatosensory (SI) Cortex of the Brain - the Homunculi

While initially the somatotopy of referred sensations was emphasized, later studies stressed the lability of these maps over time (Halligan et al., 1993) and noted that referred sensations to the phantom are not restricted to the ipsilateral side of the body (Knecht et al., 1998a; see Fig. 1.3).

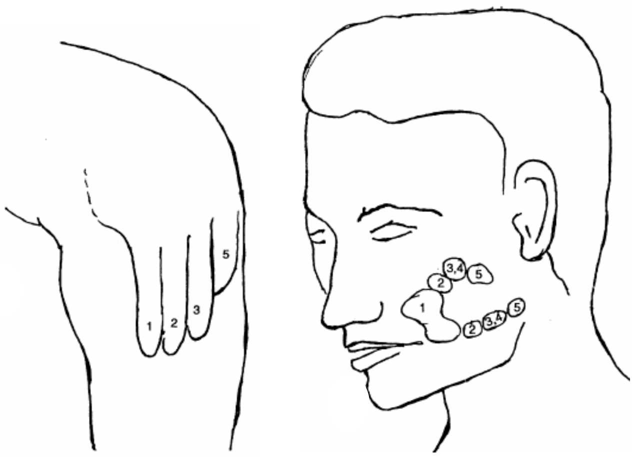


Fig. 1.2: Distribution of reference fields in patient D.S. (Ramachandran & Hirstein, 1998). Note the topographical distribution of the fingers on the stump and face area. Numbers 1 - 5 denote the individual fingers, whereas 1 denotes the thumb.

Interesting in this context are the results of a study in which referred sensations to a phantom hand were elicited by stimulation of the lower body or on the body side contralateral to amputations in two upper limb amputees. The underlying mechanisms for this referral of stimuli that are neither adjacent on the body surface not adjacent on the homunculus in primary somatosensory cortex are not clear, but were interpreted by the authors as contributions of cortical reorganization that is not restricted to the primary somatosensory cortex, but comprises secondary somatosensory cortex or subcortical areas (Grüsser et al., 2004).

Farnè and collaborators showed that this taking over of "empty" areas after amputation can be reversed after transplantation of the amputated limb. They report data from a patient receiving a graft hand who recovered good sensitivity in the graft but showed an extinction of tactile stimuli delivered to the graft when his ipsilateral cheek was stimulated simultaneously. 6 month after transplantation the face-hand extinction was no longer present. The authors interpreted this inital, but later vanishing, extinction phenomenon as a sign for the regain of a sensorimotor representation of the "new" hand, that resemled that of the lost limb. (Farne et al., 2002).

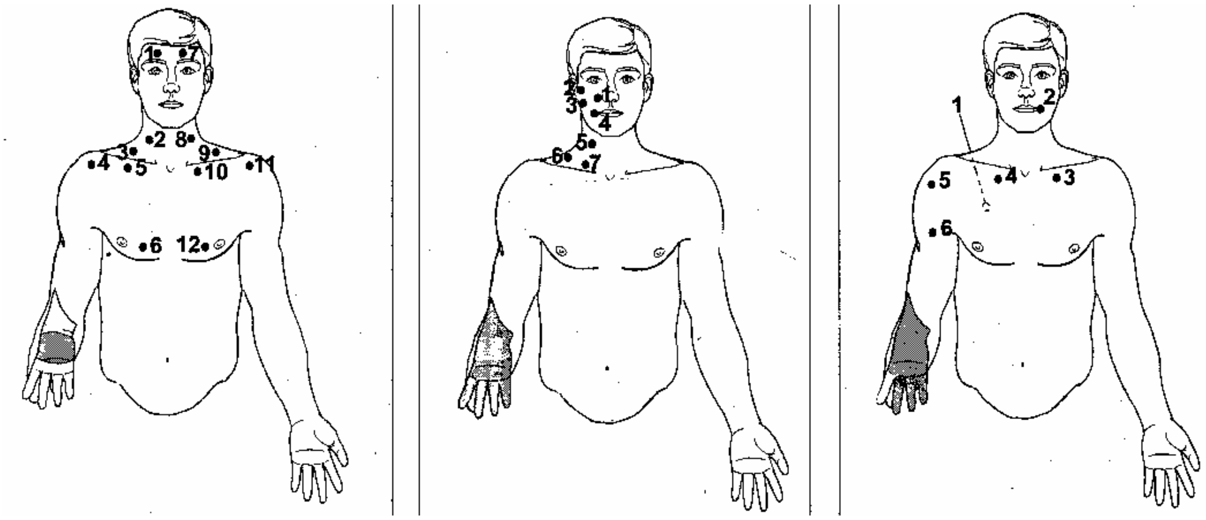


Fig. 1.3: Plasticity of mislocalization of stimulation on the body into the phantom hand (referred sensations) in one male hand amputee over the course of 3 sessions (from left to right) as described in Knecht et. al (1998). Sessions 1 and 2 were separated by 4 weeks, sessions 2 and 3 were separated by 18 months.

Intriguingly, Ramachandran & Hirstein (1998) also showed that referred sensations are modality specific: when they stimulated with hot, cold or pinprick stimuli, the referred stimuli were also experienced as hot, cold or pinpricks.

What might be seen as an analogy to referred sensations in amputees can also be found in healthy subjects - it is an experience called *Mitempfindung*, in which one single stimulation (e.g. a scratch) is felt not only on the stimulation site, but also on a site far away from this point (see Schott, 1988 for review).

Origin of Phantom Sensations

Since the first description there have been many theories on the origin of phantom limbs. Amongst them are irritation of axon terminals in the stump due to scar tissue or neuromas, psychological repression, and cortical reorganization in the brain. Today it seems clear that this complex phenomenon cannot be explained by one factor alone, but, rather, a *mulitfactorial origin* is most probable (Ramachandran and Hirstein, 1998). Factors influencing the origin and persistence of phantom sensations are peripheral factors like stump condition, somatic memories, cortical reorganization, and the existence of a genetically hardwired "neuromatrix":

- Stump condition: On the one hand, manipulation of the stump can resurrect a faded phantom in some patients and help others attenuate phantom pain. This indicates that peripheral factors can influence phantom experiences. On the other hand, it must be noted that repeated stump operations (e.g. to remove scars) do not lead to lasting relief from (painful) phantom experiences (Weinstein, 1969). Stump condition alone is thus not sufficient to explain the existence of phantom phenomena.

- Somatic memories: Pre-amputation pain, malformations of the limb, and feelings of wearing a watch or a ring are often carried over into the phantom experience. This transfer shows how fleeting somatic associations that usually will only seldom access consciousness may be recorded permanently in the brain (Ramachandran and Hirstein, 1998).

- Cortical reorganization: The human body is represented in several loci in the brain, amongst them in the primary motor (MI) and somatosensory (SI) cortices (see Fig. 1.1). In 1992 Ramachandran and colleagues suggested that phantom limb experiences may be the result of changes in cortical organization (Ramachandran et al., 1992b). The idea is that brain areas which used to represented the amputated body part are now "empty". Neighbouring areas will thus start to "invade" and functionally take over the empty areas. Modern tools like transcranial magnetic stimulation (TMS; Pascual-Leone et al., 1996) and functional magnetic resonance imaging (fMRI; Lotze et al., 1999) have helped support this idea. Flor and collaborators succeeded in demonstrating a relationship between the amount of cortical reorganization and the magnitude of phantom limb pain with magnetic source imaging, a combination of fMRI and magnetoencephalography (MEG; Flor et al., 1995). For a short explanation of the above mentioned techniques, see Insertion 2.1.

- "Neuromatrix" theory: In 1990 Ronald Melzack postulated that "a *genetically built-in matrix* of neurons for the whole body produces characteristic nerve-impulse patterns for the body and the myriad somatosensory qualities we feel" (p. 91; italics added). This neural network, or "neuromatrix", does not simply disappear because of a peripheral amputation. The neural basis of the body, though modifiable by sensory inputs, lives on in the brain giving rise to phantom sensations. Support for the neuromatrix theory comes from patients with congenitally absent limbs, who - like amputees - may be experiencing phantom sensations. If there really is something like a body image hardwired into our brain, it may explain why patients who have never actually possessed arms or legs can still have a representation of these body parts in their sensory and motor cortices and, thus, experience "intact" bodies (Melzack et al., 1997). However, it is still necessary to consider the possibility of an acquired genesis of phantom sensations in people with congenitally absent limbs. It is conceivable that the lifelong visual observation of conspecifics moving their limbs leads to a buildup of some somesthetic representation of the physically absent limb. This might happen via a mechanism of matching action observation and (implicit) action execution (Brugger et al., 2000).

Taken together, these results provide evidence for at least a partly pre-determined, but modifiable body representation, that is, a neural representation of the body that may survive drastic changes in the actual appearance of the body (e.g. amputations) and may provide the impression of an intact body that never existed (e.g. in congenital limb aplasia). As Melzack (1989, p. 4) puts it: ‘‘It is evident that our experience of the body can occur without a body at all. We don't need a body to feel a body.’’

To complete this section on phantom sensations in clinical populations, it is noted that out-of-body experiences (OBEs) may be considered as "phantoms of one's entire body" (Brugger, 2006). Accordingly, the lesions typically reported in patients reporting OBEs affect areas critical for body representations beyond those of simple primary sensorimotor representations, i.e. the parietal lobes (Blanke et al., 2004). Most likely, even OBEs reported by healthy individuals can be linked to parietal lobe irritations which temporarily affect body perception.

Chapter 2

Phantom Sensations in Healthy Volunteers

Chapter 1 introduced the phenomenon of phantom sensations and gave a short overview of the current knowledge about this striking condition. Chapter 2 discusses distinguishable components of the body representation and introduces experimental methods to manipulate corporeal awareness.

The Parietal Lobes

The parietal lobes have long been known to be important for our bodily perception (Critchley, 1953). This knowledge comes from clinical observations of patients presenting with lesions of the parietal cortex and, since the advent of modern brain imaging techniques, also from the experimental study of the intact brain of healthy volunteers. Below, I provide a short overview of the parietal lobes.

Anatomy and General Function of the Parietal Lobes

The parietal lobes are part of the cerebrum and are situated between the frontal and the occipital lobes of the brain. They are responsible for a wide range of functions, with some specialization of the left and right counterparts. Lesions of the parietal lobes can lead to sensory impairments of the contralateral body half because the parietal lobes contain the primary sensory areas of the brain (see Fig. 1.1). The *left* parietal lobe is important for several language and language associated functions. Lesions of the left parietal lobe may lead to alexia (the inability to read), agraphia (the inability to write), acalculia (the inability to perform mathematical tasks), apraxia (the inability to perform motor tasks on command, without the presence of a deficit in motor functions), and the Gerstmann-Syndrome. The existence of the Gerstmann-Syndrome is debated. Clinically, it is diagnosed if the following symptoms are present: finger agnosia (the inability to name and discriminate the fingers), left-right confusion, agraphia, and acalculia. Lesions of the *right* parietal lobe may lead to problems in spatial orientation, visuospatial perception, and to the neglect syndrome, in which patients present with inattentiveness to the left half of their environment and/or their body (Critchley, 1962).

The Parietal Lobes and Corporeal Awareness – Studies with Patients

Hints that the parietal lobes are important for bodily perception first came from patients with lesions of these structures. A striking example is seen in patients with the above-mentioned neglect syndrome. This syndrome is comprised of several symptoms, which vary in degree: patients are *inattentive* to the left part of their environment and/or the left part of their body. They will not shave the left half of their face or will leave the food on the left half of their plate untouched and complain that they are still hungry. Often *ownership* of neglected body parts is denied. The patient may instead claim that the arm attached to his left side is a prosthesis or even that the arm belongs to somebody else. This symptom, called *"somatoparaphrenia"*, is however very rare (Bottini et al., 2002). Moreover, *"extinction"*, in which a stimulus on the left side is not perceived in simultaneous, bilateral stimulation (e.g. stroking of both hands) but only in unilateral stimulation, is found in many neglect patients. It is important to note that extinction occurs although the basic sensory functions are still intact, which explains why unilateral stimulation is perceived equally well on the neglected as well as on the healthy side of the body. Often "*anosognosia"* is also encountered in neglect patients. Anosognosia originally referred to the lack of insight into one's own hemiplegia; nowadays the term is used to denote lack of insight into various neurological impairments. A patient with anosognosia may insist on being able to walk, in spite of his hemiplegia, and claim to only just now be sitting in a wheelchair because he feels too tired to walk.

Patients with hemiplegia may also show "*misoplegia"* (a dislike towards a paralyzed limb; Critchley, 1974). This dislike may even culminate in physical aggression towards the affected side (Loetscher et al., in press). Other symptoms found in parietal lobe damage may include the feelings that limbs are too heavy or too light (hyper-, hyposchematia) or a patronizing attitude towards an affected limb (personification) (Critchley, 1962).

Another striking condition, which may be observed after lesions of the right parietal lobe, are "supernumerary phantoms" - the experience of extra body parts. The patient may have the vivid impression of one (or more) spare arms or legs, which are felt very vividly and are experienced as "real limbs", belonging to the body (Bakheit and Roundhill, 2005; see Brugger, 2003 for review). Unlike patients with amputation or deafferentation phantoms, many patients with supernumerary phantoms report being able to see their phantom or exhibit other delusional elaborations of their somatosensory illusion. This implies that, compared to amputation phantoms, higher order integration brain areas participate in the generation of supernumerary phantom limbs.

The Parietal Lobes and Corporeal Awareness – Studies with Healthy Subjects

The sensory homunculus (Fig. 1.1), known to spread over the anterior part of the parietal lobe (Penfield and Jasper, 1954), is crucial for the basic perceptual qualities of human body awareness. Much wider areas, however, are involved in the mediation of corporeal awareness beyond unimodal somatosensory input. For instance, Ehrsson and co-workers showed increased brain activation in the cortices lining the left postcentral sulcus and also in the anterior part of the intraparietal sulcus during the perception of a corporeal illusion. Cells in these areas are known to have the capacity to integrate tactile and proprioceptive information from different body parts. The authors concluded that "our finding is important because it provides direct neurophysiological evidence that the parietal cortex is involved in the construction of the body image" (Ehrsson et al., 2005).

Body Representations

There are several possibilities to differentiate components of body representations. Suggestions have come from Gallagher & Cole (1995), Paillard (1999), and from Schwoebel & Coslett (2005). Each suggestion is based on clinical data and employs the terms "body *image*" and "body *schema*" to describe different components of body representation. Moreover, Schwoebel & Coslett also use the term "body *structural description*" to describe a third component of body representation. It is important to note that although the terminology used is partly the same, different authors may assign different meanings to the same term.

Gallagher & Cole (1995) argue that a clear distinction between body image and body schema is necessary to work out their functional differences and to be able to take apart their effects on the behavioral level. In their definition the body *schema* is a system of motor capacities and habits that enable movement and the maintenance of posture. The body schema is not necessarily conscious and does not refer exclusively to one's own body. The body *image* is a set of intentional states containing perceptions, mental representations, beliefes and attitudes. Unlike the body schema, the body image is conscious and is directed towards one's own body.

Paillard (1999) argues that the first step in distinguishing between a body image and a body schema is to discriminate between a “conscious awareness of one’s own body and a non conscious performance of the body” (p. 197). He suggests that two body representations exist in the brain, which are analogous to the visual “what” and “where” pathways: the body *schema*, containing information about the location of body parts (“where”) and the body *image*, which perceptually identifies body features (“what”). The body schema – which he also calls the body frame – depends largely on proprioceptive information to constantly update information about body posture. The body image is mainly supported by visual information to help maintain a central representation of the body.

According to Schwoebel & Coslett (2005), the body *schema* is an "on-line sensorimotor representation" (p. 543). It is comprised of information coming from different sensory systems like the visual, vestibular and proprioceptive systems. Information from these systems are integrated and build up a dynamic representation of the body which is constantly updated and codes for the position of body parts in relation to each other. The body *image* is a "semantic and lexical representation of the body" (p. 544). It contains the names of body parts and the knowledge about the function of body parts and which artifacts may be manipulated with which body part. Last but not least, the body *structural description*, a "topological map of the body" (p. 544), contains information about the boundaries of body parts and their anatomical relationship with respect to each other. Unlike the body schema the body structural description is considered to be built mainly from visual information.

How to Differentiate Components of Bodily Representations.

To make a clear distinction between body image and body schema and clarify their functional interrelations, Gallagher & Cole (1995) describe the case of deafferented patient IW, who after peripheral neuropathy, lost the sense of touch from the neck down. As in their definition where proprioception is the major functional aspect of the body schema, IW presents with a grossly disturbed body schema and, as a result, is not able to execute unattended movements. Over the course of several month, however, he learned to execute movements and to maintain posture under constant visual observation of his body, i.e. he was able to compensate for a loss of the preconscious body schema with the help of the conscious body image.

In support of his theory that the body representation may be split into a body image and a body schema, Paillard (1999) describes two patients – one with a central and one with a peripheral condition – who both present with a severely disturbed body perception:

- Patient RS suffered an ischemic stroke after occlusion of the left posterior parietal artery. After the incident she presented with incomplete right-sided hemianopia, hemianacousia, and hemianesthesia. Her joint position sense, thermal, and pain sensations were absent on the right side and she was unable to detect static tactile stimulation on her lower right arm and hand. Nevertheless - and much to her own surprise - she was able to point accurately with her intact hand to a point stimulated on her affected right hand. She was able to localize stimuli without consciously detecting them – a phenomenon termed “blind touch” (Paillard, 1999, p. 201) in analogy to “blind sight”, the ability of centrally blind patients to correctly point to visual stimuli they do not consciously perceive (Stoerig and Cowey, 1997).

- Patient GL has lost her ability to perceive touch, vibration, pressure and kinesthesia, probably due to two episodes of the Guillain-Barré-Syndrome. As confirmed by biopsy, she has lost her large diameter sensory fibers, but can still detect pain and temperature as her small diameter sensory fibers were spared by the illness. Moreover, her motor fibers are intact, so she can move almost normally as long as visual control of her limbs is possible. Unlike Patient RS, GL consciously perceives cold stimuli applied to various sites over her body, but is unable to point correctly to the stimulated site on her body – although she is able to correctly identify the stimulated body part verbally and is also able to point to the correct body part on pictures depicting body parts.

From experiments with these two patients, Paillard concluded that there is a double dissociation in the ability to detect and to localize stimuli on the body. Patient RS was able to direct her healthy hand to the stimulated body part according to her body schema without perceiving the stimulus. Patient GL correctly identified a stimulated body part verbally or on a picture according to her body image, although she was unable to point to the body part on her actual body.

To differentiate components of bodily representations, Schwoebel & Coslett (2005) examined 70 patients with a first time single-hemisphere stroke. Patient selection was not based on behavioral or lesion criteria, as the goal of the study was to determine the prevalence and anatomic bases of disorders of body representation. Participants had to solve several tasks assessing particular domains of the body representation; solving the tasks required non-verbal responses, reacting to color pictures of body parts. The performance of these 70 stroke patients was compared to the performance of an age-matched healthy control group comprised of 18 participants. The study consisted of 7 tasks to be solved, among them were:

- Hand laterality task: Subjects were shown pictures of hands in different positions (e.g. palm facing up vs. palm facing down) and had to indicate if the hand shown was a left or a right hand.

- Localization of tactile input: Patients were blindfolded and various body sites were stimulated with suprathreshold stimuli applied with a brush. Patients then had to point to the stimulated body part on a mannequin.

- Matching a body part to clothing and objects: An item of clothing was presented along with pictures of four body parts. Patients had to indicate which body part was most closely associated with the item of clothing displayed.

Following a principal component analysis, the seven tasks revealed three factors, which the authors interpreted as the three components of the body representation: the "body schema", the "body structural description", and the "body image". Schwoebel & Coslett found that 51% of their patients were impaired on at least one domain of their body representation and that there was a triple dissociation between the three measures of body representation (Schwoebel and Coslett, 2005).

How does the Brain Recognize Parts of its own Body?

Being able to distinguish different components of the body representation can be helpful for understanding and explaining intriguing clinical conditions like those described above by Paillard (1999). But how does one actually know what does and what does not belong to one’s own body? For example, how do I know that my arm is actually *my* arm and not my aunt’s arm, or how do I know that my arm is part of my body, but my sleeve, which is in constant contact with my arm and actually moves like my arm, is not? Experiencing a limb as belonging to one's own body needs a multisensory integration of stimuli coming from various sensory systems like the visual and proprioceptive systems. A likely candidate for this integration is the premotor cortex, which is connected to visual and somatosensory areas in the parietal cortex and to frontal motor areas. Moreover, it is known that premotor neurons represent both the seen and the felt position of a hand - at least in monkeys (Graziano, 1999; see Ladavas et al., 2000 for observations in human individuals). Using the Rubber Hand Illusion (RHI), which is explained below, Ehrsson and colleagues reported with the help of fMRI that activity in the premotor cortex of the brain is associated with the feeling of ownership of a seen rubber limb. They stated that "activity in this area [the premotor cortex] is associated with the subjective experience that the body one sees belongs to oneself" (p. 876). Moreover, the authors demonstrated that the left premotor cortex showed enhanced activation only after the onset of the RHI and that the bilateral premotor cortex activation coincided with the subjective strength of the illusion (Ehrsson et al., 2004).

Bottini and collaborators describe a single-case study of a 77-year-old, right-handed woman who suffered from a right-sided hemorrhage affecting subcortical structures and the white matter underlying the cortex of the insula, superior temporal gyrus, parietal operculum, and the pre- and postcentral gyri. The patient, who suffered from left-sided hemiparesis and anosognosia, among other symptoms, firmly denied ownership of her left hand. Instead, she assigned her hand to her niece, the above-mentioned "somatoparaphrenia" (p. 21). The patient was able to perceive touches delivered to her hand, but only when assuming that is was her niece's hand being touched (Bottini et al., 2002). The ability to perceive touch is thus not sufficient to generate a sense of ownership.

Methods to Manipulate Body Representations in Healthy Volunteers

This section explains the three methods I used during the course of my thesis to manipulate the body experience of my participants. Moreover, local anesthesia, a method not employed in my own studies, is described.

Vibration Illusions

In 1988 James Lackner published a paper describing several illusions elicited by vibrating various muscle tendons of his subjects (Lackner, 1988). Among others were the illusion of a growing nose ("Pinocchio-Illusion"), a growing head ("Conehead"), and sensations of unusual posture changes like sinking into the floor (see Fig. 2.1).

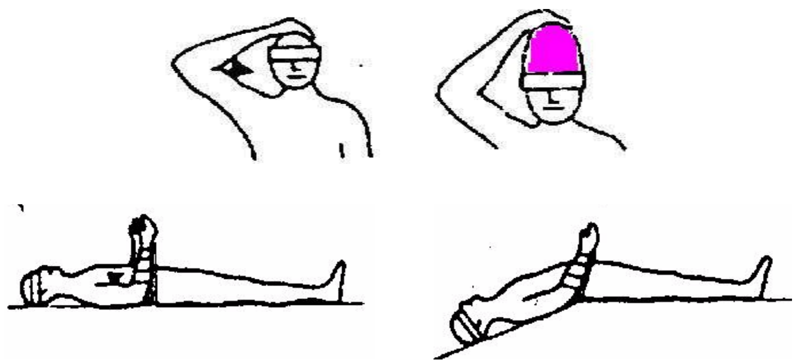


Fig 2.1: Examples of vibration illusions as described by Lackner (1988). Left side: Stimulation site marked by black triangle, right side: perceptual experience.

All of these illusions are based on the same principle: the participant needs to be blindfolded, then one (or several) of his muscle tendons – the organs connecting the muscle to the bone (see Fig. 2.2) – are vibrated with a frequency of about 80 to 100 Hz. For vibration illusions only tendons attached to a joint are being stimulated. The frequency band of 80 to 100 Hz has proven to most reliably elicit vibration illusions – possibly because up to a frequency of 80 Hz there is a one-to-one correspondence between the muscle spindle discharges and the vibration (Roll et al., 1989). As a consequence of the vibration, the muscle tendon signals activity to the brain, which in turn interprets the incoming signal as muscle activity, or more precisely, as a shortening of the respective muscle. The brain's assumption of the muscle shortening induces the illusion that the limb controlled by the muscle is actually revolving around its joint. The vibration of the biceps brachii tendon, for example, which attaches the upper arm muscle to the elbow joint, induces the illusion that the arm is extending (i.e. revolving around the elbow).

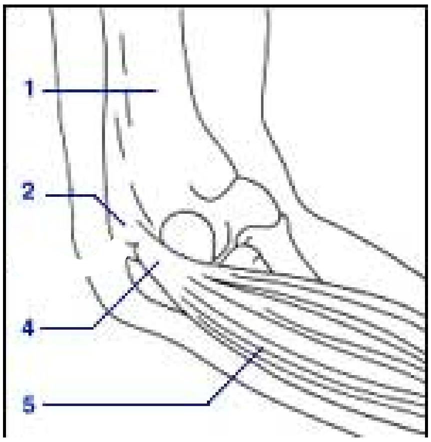


Fig. 2.2: Anatomy of the lower arm tendon at the elbow.
1 = bone of upper arm
2 = insertion of tendon
4 = tendon
5 = lower arm muscle

In blindfolded subjects the illusions of movement are very convincing. In some cases the extent of the movement is even felt to extend beyond the physical limitations imposed by the joint. Matching experiments, in which participants had to match the position of the vibrated arm with the non-vibrated arm, were conducted to show the extent of the illusory movement (Goodwin et al., 1972).

If subjects are instructed to hold on to a specific body part while experiencing the movement illusion, the shape of this body part may be altered with the movement. To elicit the Pinocchio-Illusion, participants are instructed to hold on to their nose while one of their arms is being vibrated. When the illusion of arm extension sets in, the brain is confronted with two conflicting pieces of information: on the one hand, the convincing information of an extending arm and, on the other hand, with proprioceptive feedback from the nose and fingers indicating that these two body parts are in contact. The brain attempts to resolve this conflict and recalibrates the size of the touched body part accordingly, hence the Pinocchio-Illusion. The same principle holds true for the Conehead and the other illusions described by Lackner.

Ehrsson and colleagues conducted a fMRI experiment studying brain activation during a vibration illusion that induces the feeling of a shrinking waist (see Fig. 2.3, Ehrsson et al., 2005). There are no specialized skin, joint or nerve receptors for size and shape of body parts as there are for movement, touch, temperature or pain. Thus the question is: how does the brain compute the size and shape of the body as a whole and the size and shape of its parts? As specific receptors for the perception of the size of body parts are lacking – which is supported by the fact that the perceived size and shape of body parts can change during anesthesia and vibration illusions – the brain is thought to infer the size of a body part by integrating and comparing signals from different body parts and also from visual information from the body.

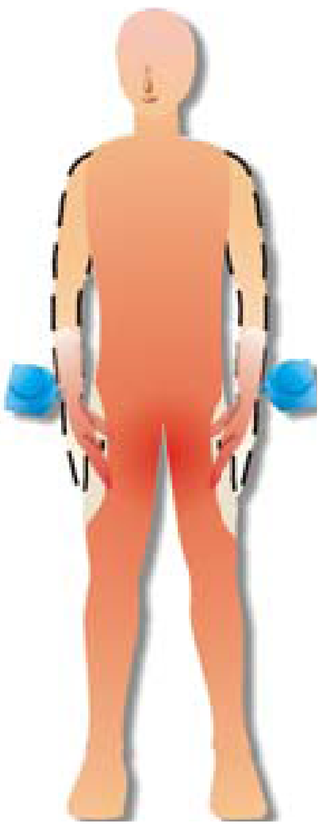


Fig 2.3: Vibration of the wrist tendons while the hands touch the waist, induces the feeling of a shrinking waist. Although from this original drawing it looks more like that the thighs were vibrated. (Ehrsson et al., 2005)

The size of a body part is probably represented in a relative sense, that is, relative to the size of other body parts and also relative to the size of objects in the external environment. During the experience of the shrinking waist Ehrsson and colleagues' data showed brain activation in the cortices lining the left postcentral sulcus and also in the anterior part of the intraparietal sulcus. The activity was correlated with the subjective degree of shrinkage in the waist. The activity in the illusion condition was compared to several control conditions. In one of the control conditions the skin directly over the bone was vibrated, without stimulation of the tendon. In another control condition the tendon was correctly vibrated, but the hands were not touching the body; thus the stimulation elicited the illusion of moving hands, but without the illusion of a shrinking waist. By comparing the brain activity in the illusion condition with the brain activity in these control conditions, the authors concluded that the activity in the illusion condition "probably reflects the neuronal computations associated with the recalibration of the size and shape of the waist. Thus, these parietal areas are likely to be important for the construction of the body image" (Ehrsson et al., 2005, p. 2203).

De Vignemont and colleagues examined the notion that there are no specialized receptors for body size in an astonishing experiment. With the help of vibration stimuli they led subjects to believe that their index finger was growing. At the same time, the participants had to judge the distance of stimuli delivered successively to their forehead and to the finger via two solenoids. The task was to determine if the distance between the solenoids was bigger on the finger or on the forehead. It turned out that the perceived distance on the finger varied with perceived finger size, so if the vibration induced the feeling of an elongated finger, the distance on the finger was judged to be greater than on the forehead and vice versa (de Vignemont et al., 2005).

Virtual Reality Box

In 1996 Ramachandran and his co-worker (Ramachandran and Rogers-Ramachandran, 1996) introduced a device they called the “virtual reality box”. It consisted of a box with two openings on the longer side and a vertical mirror in the middle of the box. The two openings allowed the subject to insert his arms into the box. Participants in this study were unilateral upper limb amputees who were experiencing phantoms. The amputees were instructed to place their phantom on one side of the mirror and their intact hand on the other side. When the amputee then looked into the mirror reflecting his intact hand, his brain was made to believe that he could actually see his phantom – the amputated limb was visually resurrected.

By being provided with visual feedback from the phantom, some of the examined amputees were able to regain motor control over their formerly "frozen" phantoms. Through this, some of them were able to find relief from the phantom pain they were experiencing: a common experience in hand amputees is the description of excruciating phantom pain that feels as if nails were digging into the palm - like they do when the hand is formed into a fist. This pain is believed to be caused by motor commands sent from the brain to the hand, which are never verified due to the deafferentation of the hand. Therefore, the signals from the brain start to increase, thus causing the feeling of a cramped fist with the accompanying feeling of fingers digging into the palm. Through the simple trick of visual feedback, this vicious circle could be broken in some of the amputees, which allowed them to "open the fist", thus relieving their phantom pain.

Rubber Hand

The rubber hand illusion (RHI) was first described by Botvinick & Cohen (1998). The authors described a compelling illusion that led people to believe that they could actually feel the touch delivered to a rubber hand. To elicit the illusion Botvinick & Cohen seated their subjects at a table, the arm resting on the table. The arm was covered so that it could not been seen by the participant and, instead, a realistically looking life-size rubber arm was placed next to the participant's hidden real arm (Fig. 2.4).

Fig 2.4: Set up for the Rubber Hand Illusion experiment

Participants were instructed to look at the rubber hand, and the visible rubber hand and the invisible real hand were stroked repeatedly in synchrony but arhythmically with little paintbrushes. After ten minutes subjects filled out a questionnaire (Tab. 2.1), assessing nine possible reactions to the stimulation. Most participants agreed strongly with the first three questions, confirming they had actually felt the brush touches as originating from the fake rubber hand.

Since the original study, the RHI has been studied extensively with various techniques like functional magnetic resonance imaging (Ehrsson et al., 2004, as described in the section above) and the galvanic skin response (Armel and Ramachandran, 2003, see Insertion 2.1). Moreover, several authors attempted to describe the circumstances most likely to elicit a (convincing) illusion. However, opinions on this question differ. Armel & Ramachandran (2003) showed that the illusion occurs in situations were the rubber hand is placed in a way matching the position of the real hidden hand (usually called the "congruent" condition). But they were also able to elicit the illusion – even if not as strongly as in the congruent condition – in incongruent conditions, namely, when the rubber hand was placed about a meter in front of the body, when it was rotated by 90 degrees and even when the realistic rubber hand was replaced by a shoe (Armel & Ramachandran, 2003; Ramachandran & Hirstein, 1998). Tsakiris & Haggard (2005), in contrast, claimed that incongruent rubber hand postures or identities will not lead to self-attribution of a rubber hand. Neither of the authors offered an explanation for this discrepancy.

Tab. 2.1: Questionnaire used in the rubber hand study by Botvinick & Cohen (1998)

During the experiment there were times when:

- It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched.
- It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand.
- I felt as if the rubber hand were my hand.
- It felt as if my (real) hand were drifting towards the right (towards the rubber hand).
- It seemed as if I might have more than one left hand or arm.
- It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.
- It felt as if my (real) hand were turning „rubbery".
- It appeared (visually) as if the rubber hand were drifting towards the left (towards my hand).
- The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.

Local Anesthesia

Anesthesia can be interpreted as a transient form of amputation. During anesthesia signals coming from the periphery no longer reach the brain ("deafferentation"), and signals from the brain no longer reach their destination in the periphery ("deefferentation"). This simulates the condition in an amputation: after a limb has been removed the brain no longer receives signals coming from that limb and signals from the brain can no longer reach the limb. Anesthesia can be applied in several ways, for example, through medical block of limbs or certain parts of the spinal cord or by cutting of the blood circulation in a limb (“pressure cuff anesthesia”). As the first method involves the application of medication and the second is rather painful, they were not used in the present thesis. The effects of anesthesia induced by medication are often studied in patients who are undergoing anesthesia for medical reasons anyway. Paqueron and colleagues examined 36 patients undergoing upper limb, lower limb or spinal anesthetic block for orthopedic surgery. During the anesthesia, sensory and motor functions were assessed at regular intervals. Changes concerning the size and shape of the anesthetisized limb occurred in a majority of the patients; illusions of swelling, elongation or shortening of the limb were most prominent. The illusions coincided with an impairment of warm, cold and pinprick sensations. From their findings the authors concluded that either the small myelinated or the unmyelinated sensory fibers (which carry information about pain and temperature) are responsible for the cortical representation of the limb. Some patients in their study even experienced conflicting sensations, like the swelling of a limb which at the same time was felt to be missing. The sense of ownership for the anesthetisized limb was also impaired in some cases. The described alterations in shape and size were different from alterations in posture, which occurred at a different time course and were influenced by visual feedback. The authors concluded from this that the perception of body shape and the perception of body posture are derived from separate plastic models (Paqueron et al., 2003). The type of phantom sensations Paqueron and colleagues described is known to most people: it is exactly what happens after receiving anesthesia at the dentist. After injecting the anesthetic drug, the jaw, cheek and/or lips (depending on the site of injection) feel swollen. The feeling is so convincing that it can only partially be relieved by a look into the mirror. Although visual feedback shows the "regular" face, the perception of swelling persists.

Functional Magnetic Resonance Imaging (fMRI)

FMRI uses radio waves and a strong magnetic field to provide detailed pictures of the brain. FMRI is used to identify regions of the brain where blood vessels are expanding and extra oxygen is being delivered - a sign that this part of the brain is processing information or giving commands to the body.
The main advantages of fMRI are that there are no potentially harmful interventions like the injection of radioactive isotopes or the application of x-rays required, the scan time may be very short, and the resolution of the image is very good.
During the fMRI measurement, the patient performs a particular task. The metabolism in the area of the brain responsible for this task increases and the signal in the fMR image will change. By performing specific tasks that correspond to different functions, it is possible to locate the corresponding area of the brain that is associated with the function.

Magnetoencephalography (MEG)

MEG is the non-invasive, external measurement of the magnetic fields produced by the electrical activity in the brain. The measured magnetic fields are not effected by the skull and the tissue surrounding the brain, therefore the signals are much less distored than in electroencephalography (EEG). MEG is often used in the presurgical assessment of epilepsy patients to pinpoint the source of epileptoform activity in the brain.

Galvanic Skin Response (GSR)

GSR measures the skin conductivity from the hand. The conductivity of the skin is coupled with the activity of the sweat glands, which depend on the activity of the sympathetic nervous system and cannot be deliberately manipulated. The GSR is a measure for the baseline activity of the sympathetic nervous system. It is highly sensitive to emotional changes of the sympathetic nervous system and is at times being used as a lie detector.

Transcranial Magnetic Stimulation (TMS)

TMS uses rapidly changing magnetic fields to induce electric fields in the brain. It may be used to stimulate or suppress the activity of the area of the brain over which it is applied, thereby it can facilitate or disrupt the solving of tasks.

Insertion 2.1: fMRI, MEG, GSR and TMS "in a nutshell"

Goal of this Thesis

Although our knowledge about phantom sensations is steadily growing, we still know very little about their genesis. By better understanding the body representation of healthy volunteers, we hope to better understand the body representation of patients with phantom sensations and eventually help patients who are experiencing phantom pain, which is to date mostly unresponsive to conventional therapy (e.g. pain medication). Thus, the goal of this thesis was to achieve an improved understanding of the body representation of able-bodied persons. To reach this goal I manipulated healthy participants' experience of their body with various techniques, which were described above.

More specifically, I was interested in

- investigating the individual differences in the perception of bodily illusions in healthy subjects

- examining a phenomenon that is known in healthy volunteers as well as in amputees (the perception of a single touch stimulus in two places at once) to uncover possible common mechanisms

- studying the effects of cross-modal interference between vision and touch in a subject who has lost conscious touch perception due to peripheral deafferentation

- analyze whether a bodily illusion that has been studied extensively in able-bodied subjects (the rubber hand illusion) can be elicited in hand amputees.

Chapter 3

Empirical Studies

This chapter contains my own experimental findings. Where applicable, a prior publication in a peer-reviewed journal is mentioned.

Study 1: The Pinocchio-Illusion

During pilot experiments prior to this study I noted large individual differences in the proneness to this illusion. The literature on this specific illusion as well as the literature on other body illusions did not note these obvious differences between subjects. Thus, I tried to uncover why these individual differences might exist and if they are related to individual proneness to experience spontaneous body schema alterations in everyday life. The study had two goals: (1) To provide quantitative data on healthy participants' responsiveness to experimentally induced phantom sensations. (2) To explore personality correlates of an individual's inclination to experience experimentally elicited phantom sensations. The study was published in Body Image: Burrack, A. & Brugger, P. (2005). Individual differences in susceptibility to experimentally induced phantom sensations. *Body Image, 2*, 307-313.

Individual Differences in Susceptibility to Experimentally Induced Phantom Sensations

Introduction

The representation of the human body by the central nervous system is a topic that enjoys increasing attention from the neurosciences. Classic concepts of the ''body schema'' as a unitary function giving rise to corporeal awareness (Critchley, 1953) have long been replaced by more sophisticated models of bodily representations that consider basic sensorimotor factors alongside higher cognitive and affective processes in the experience of our body (e.g. Coslett et al., 2002; Melzack, 1990). A vast literature on phantom sensations after loss or deafferentation of a limb has revealed that the representation of one's body is more plastic and flexible than previously assumed (Ramachandran and Hirstein, 1998).

The relatively few studies on the experimental evocation of phantom sensations in healthy volunteers have produced further evidence for the short-term plasticity of bodily representations. One way to induce a phantom limb percept in able-bodied subjects is by way of vibratory stimulation of muscle tendons (Jones, 1988, for overview). For instance, vibration of the biceps tendon of a bent and immobilized arm in a blindfolded subject produces an illusory movement of the lower arm around the elbow. Specifically, the arm is experienced to move into extension and is finally felt at some location in extracorporeal space. An intriguing modification of the basic procedure of tendon vibration was introduced by Lackner (1988). This author described a phantom nose illusion (‘‘Pinocchio illusion’’, Fig. 3.1) in subjects who had their biceps tendon vibrated while the fingers of the vibrated arm touched the tip of their nose. Apparently, the brain bridges the gap between fingers felt at a distance in front of one’s face and the tip of one’s nose by filling in the illusory gap with a prolongation of the nose (or, alternatively, of the fingers, as reported by some subjects; Lackner, 1988). The physiological aspects of vibration-induced arm, nose or finger phantoms have repeatedly been investigated (Goodwin et al., 1972; Lackner, 1988; Naito et al., 2002), but participants’ overall responsiveness cannot be judged from these reports. Also, there is little systematic research on interindividual differences in the susceptibility to experimentally induced phantom sensations (Juhel and Neiger, 1993, for an exception).

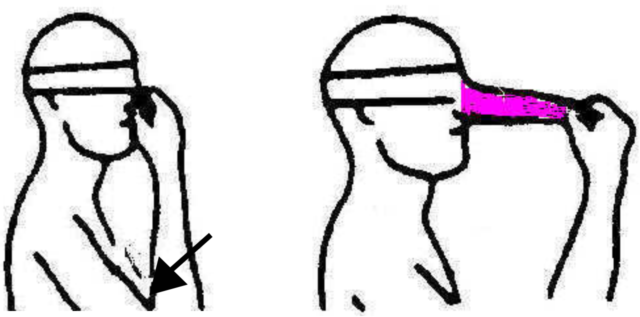


Fig 3.1: Pinocchio-Illusion. Left side: Experimental setup, stimulation site on inside of ellbow marked by arrow; right side: perception.

The present study pursued two goals: First, to provide quantitative data on healthy participants’ responsiveness to experimental procedures eliciting phantom sensations. Second, to explore potential personality correlates of an individual’s inclinedness to experience alterations in corporeal awareness in a controlled situation. Specifically, we investigated two vibration-induced illusions: (1) the illusion of arm extension and (2) the Pinocchio illusion. These were studied in relation to the frequency of body schema alterations spontaneously experienced during everyday life. In some participants, successful evocation of these two illusions was also studied in relation to cognitive style. We predicted positive correlations between the susceptibility to experimentally induced bodily illusions and (a) the frequency of spontaneously experienced body schema alterations and (b) a low need for cognitive structure.

Method

Participants

Thirty-two participants (18 women) gave written informed consent to participate in the study, which had been approved by the local ethics committee. Their mean age was 26.8 years (SD = 6.8 years). Only five participants had less than 12 years of schooling. None of the participants had a history of neurologic or psychiatric disease or developmental disorders (Campbell, 2000). Twenty-seven participants were right-handed (Chapman and Chapman, 1987). All participants were recruited by flyers or personal contact on local university grounds, and the majority were students.

Procedure

Questionnaires

Frequency of spontaneously experienced body schema alterations in everyday life was assessed with the 21-item German version of the Perceptual Aberration (PA) Scale (Chapman, Chapman, & Raulin, 1978; for normative data see Bailer et al., 2004). Sample items are: ‘‘I can remember when it seemed as though one of my limbs took on an unusual shape’’, keyed true; ‘‘I have never felt that my arms or legs have momentarily grown in size’’, keyed false. The 22 participants tested last were also administered Keller et al.’s (Keller et al., 2000) German version of the 14-item Need for Cognition (NFC) Questionnaire (Cacioppo and Petty, 1982); sample items: ‘‘It’s enough for me that something gets the job done, I don’t care how or why it works’’; ‘‘Thinking is not my idea of fun’’. Each item had to be rated on a scale from 1 (‘‘strongly disagree’’) to 7 (‘‘strongly agree’’).

Illusory Arm Extension

Participants were comfortably seated at a table wearing occluded glasses to prevent vision of the vibrated arm (Lackner, 1988). Their arms were positioned in arm rests (angle at elbow approx. 95 degrees) and had to be kept as relaxed as possible. The biceps brachii tendon of their dominant arm was then vibrated at about 100 Hz with a standard physiotherapy vibrator (Novafone GmbH, Fellbach, Germany). As soon as a movement of the vibrated arm was experienced, participants were instructed to say ‘‘Now!’’, and this latency was recorded by the experimenter. Vibration was stopped after 50 s, and participants rated the magnitude of any experienced arm extension on a 4-point scale and the vividness of the illusion on a 3-

point scale. This procedure was repeated five times, with the amplitude of the vibration increasing from trial to trial to a maximum of 4 mm.

Pinocchio Illusion

Only the 30 participants who experienced an illusion in at least one of the six trials on illusory arm extension participated in this experiment. Their dominant arm was kept in an arm rest, the non-dominant arm rested comfortably in their lap. Participants were instructed to touch the tip of their nose with the tip of the index finger of their dominant hand. Again, both arms were to be kept as relaxed as possible during the subsequent vibration of the biceps brachii tendon of the dominant arm with a frequency of about 100 Hz. Participants were required to report the onset of any change in sensation in face, head or hand by saying ‘‘Now!’’ so that the time until the onset of an illusory percept could be recorded. After 1 min, vibration was stopped, and those participants who had signaled a change in shape or size of a body part had to report where this change was felt and estimate the size of the change in centimeters. Finally, as in the arm extension experiment, the vividness of the impression of any noted change had to be rated on a 3-point scale. Again, this procedure was repeated five times with vibration amplitude increasing to a maximum of 4 mm.

Results

Data were analyzed using SPSS, version 12.0 (SPSS Inc., Chicago, IL). Results are displayed in descriptive form in Table 3.1.

Questionnaire data

PA and NFC scores were uncorrelated (Spearman ρ = -.17, $p > .4$). A low (n = 20; PA ≤ 2) and a high PA-group (n = 12; PA > 2) and a low (n = 11; NFC > 33) and a high NFC-group (n = 11; NFC ≤ 33) were created by splits at the respective median scale scores. Note that, on the PA scale, high scores indicate a high frequency of body schema alterations and on the NFC scale, high scores indicate a low Need for Cognition.

Illusory Arm Extension

Thirty out of the 32 participants experienced an illusory arm extension at least once during the six stimulation trials. For each trial, the extent of the illusion was coded from 0 (no movement sensation) to 3 (arm extension larger than 180 degrees), values of 1 and 2 indicating an illusory extension of less than 180 or equal to 180 degrees, respectively. An ANOVA of the interval-scaled latency data with gender and PA-group as the factors revealed neither main effects nor a significant interaction (all F -values ≤ 2.6, p-values $> .1$). Non parametric Mann-Whitney tests were calculated for illusion extent and vividness ratings with gender and PA-group as grouping variables. No effects emerged for the variable extent (gender: $U = 93.00$, $p = .19$; PA-group: $U = 80.00$, $p = .11$). For vividness the results were significant with gender as the grouping variable ($U = 69.50$, $p = .03$), with women rating the vividness of the experienced illusion higher than men. Raw scores on the PA scale were positively correlated with rated vividness of arm extension ($\rho = .38$, $p < .05$) and tendentially negatively correlated with the latency variable ($\rho = -.32$, $p = .07$). The correlation with illusion extent was nonsignificant ($\rho = .18$, $p > .3$). For the reduced population of 22 participants, who had been administered the NFC questionnaire, analogous Mann-Whitney tests were calculated with NFC-group as grouping variable. Participants in the high NFC-group rated illusion vividness higher than did those in the low NFC-group ($U = 30.50$, $p < .05$). There were no significant correlations between raw scores on the NFC scale and the three parameters of the illusion of arm extension (absolute ρ-values $\leq .37$, $p \geq .1$).

Pinocchio Illusion

Only 8 out of the 30 participants whose arm was vibrated while they touched the tip of their nose described a Pinocchio illusion in the narrowest sense, i.e. the unequivocal feeling of an elongation of the nose. Twelve additional participants described unspecific size changes, predominantly in the fingers, in at least one of the six trials. For each trial, the extent of the illusion was coded from 0 (no Pinocchio illusion) to 2 (clear nose elongation), a value of 1 indicating an unspecific change in size or shape of either fingers or nose. An ANOVA of latency data with gender and PA-group as the factors revealed neither main effects nor a significant interaction (all F-values ≤ 1.0, p-values $> .4$). Non-parametric Mann-Whitney tests for illusion extent and vividness ratings did not produce any significant effects ($U = 5.5$, $p > .4$).

While the correlation between raw scores on the PA scale and illusion latency was clearly not significant ($\rho = -.01$, $p > .9$), there was a trend for higher PA scores to be associated with a greater illusion extent ($\rho = .27$, $p = .13$) and a higher vividness rating ($\rho = .27$, $p = .15$). Inspection of the scattergram revealed that these trends were significant for men ($\rho = .71$, $p < .02$ and $\rho = .73$, $p < .02$, respectively), but not for women (absolute ρ-values $\leq .08$, $p \geq .9$).

Calculation of a Mann-Whitney test was not possible with the NFC-group as grouping variable, since all subjects who experienced the Pinocchio illusion were in the high NFC-group. Raw scores on the NFC scale were negatively correlated with illusion extent (ρ = -.45, p = .05), but uncorrelated to latency and rated vividness of the illusion (absolute ρ-values ≤ .37, $p \geq .1$).

Latency of the Pinocchio illusion was significantly longer than latency for the illusion of arm extension (t = 6.2, p < .001) and rated Pinocchio vividness was significantly lower than rated vividness of the illusion of arm extension (t = 2.3, p < .05).

Tab. 3.1: Questionnaire data and descriptive statistics of illusory arm extension and Pinocchio illusion

<table>
<tr><th colspan="2">Questionnaire Data</th><th colspan="5">Illusion of Arm Extension</th><th colspan="4">Pinocchio Illusion</th></tr>
<tr><th colspan="2"></th><th></th><th>N</th><th>mean (SD) latency (sec.)</th><th>mean (SD) extent (3-point scale)</th><th>mean (SD) vividness (3-point scale)</th><th>N</th><th>mean (SD) latency (sec.)</th><th>mean (SD) extent (cm)</th><th>mean (SD) vividness (3-point scale)</th></tr>
<tr><td colspan="2">PA-Scale</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>N</td><td>32</td><td rowspan="3">Low PA-Group</td><td rowspan="3">20</td><td rowspan="3">9.53 (7.39)</td><td rowspan="3">1.14 (.55)</td><td rowspan="3">1.27 (.65)</td><td rowspan="3">4</td><td rowspan="3">20.80 (15.34)</td><td rowspan="3">7.71 (12.87)</td><td rowspan="3">1.62 (.34)</td></tr>
<tr><td>mean</td><td>2.5</td></tr>
<tr><td>SD</td><td>2.4</td></tr>
<tr><td>range</td><td>0-10</td><td rowspan="2">High PA-Group</td><td rowspan="2">12</td><td rowspan="2">6.37 (3.45)</td><td rowspan="2">.80 (.36)</td><td rowspan="2">1.62 (.38)</td><td rowspan="2">4</td><td rowspan="2">23.39 (10.55)</td><td rowspan="2">1.04 (.67)</td><td rowspan="2">1.41 (.42)</td></tr>
<tr><td>median</td><td>2</td></tr>
<tr><td colspan="2">NFC-Scale</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>N</td><td>22</td><td rowspan="3">Low NFC-Group</td><td rowspan="3">11</td><td rowspan="3">10.49 (4.62)</td><td rowspan="3">1 (.52)</td><td rowspan="3">1.17 (.66)</td><td rowspan="3">0</td><td rowspan="3">--</td><td rowspan="3">--</td><td rowspan="3">--</td></tr>
<tr><td>mean</td><td>39.9</td></tr>
<tr><td>SD</td><td>15.8</td></tr>
<tr><td>range</td><td>17-69</td><td rowspan="2">High NFC-Group</td><td rowspan="2">11</td><td rowspan="2">8.37 (8.75)</td><td rowspan="2">1.12 (.64)</td><td rowspan="2">1.64 (.35)</td><td rowspan="2">4</td><td rowspan="2">27.38 (13.47)</td><td rowspan="2">7.75 (12.84)</td><td rowspan="2">1.67 (.27)</td></tr>
<tr><td>median</td><td>33.5</td></tr>
<tr><td colspan="2" rowspan="3"></td><td>Female Participants</td><td>18</td><td>7.07 (7.0)</td><td>.94 (.36)</td><td>1.61 (.41)</td><td>6</td><td>22.46 (12.62)</td><td>5.67 (10.46)</td><td>1.52 (.43)</td></tr>
<tr><td>Male Participants</td><td>14</td><td>9.85 (4.63)</td><td>1.11 (.66)</td><td>1.14 (.68)</td><td>2</td><td>21.82 (13.32)</td><td>.49 (.11)</td><td>1.5 (.24)</td></tr>
<tr><td>All Participants</td><td>32</td><td>8.2 (6.2)</td><td>1.0 (0.5)</td><td>1.4 (0.6)</td><td>8</td><td>22.7 (9.8)</td><td>4.4 (9.1)</td><td>1.0 (0.8)</td></tr>
</table>

PA = Perceptual Aberration, NFC = Need for Cognition

Discussion

We attempted to elicit two body schema illusions, vibration-induced arm extension (Jones, 1988) and nose elongation (‘‘Pinocchio illusion’’; Lackner, 1988) in healthy volunteers. It took participants longer to experience an elongation of their nose than an extension of their arm. This finding reflects the fact that in order to feel a phantom nose, one has first to feel a phantom arm, that is, an illusory extension of one’s vibrated arm. Vividness of the Pinocchio illusion was less pronounced than vividness of the arm extension. Although plausible, the higher susceptibility to experience an illusory arm extension (30 out of 32 participants) compared to nose elongation (8 out of 30 participants) has not yet been quantitatively assessed in a within-subject design. Our data show that average participants’ responsiveness to vibration-induced phantom sensations may not be as pronounced as one might expect from previous studies (Lackner, 1988).Unlike this earlier research, mainly concerned with physiological processes accompanying phantom sensations, our primary interest were individual differences in the susceptibility to these illusions. We found that the vividness for the experienced arm illusion was generally rated higher by the female than by the male participants, which to our knowledge has not been described before and for which we cannot offer a ready explanation.

Higher PA scores were weakly but significantly correlated with participants’ rated vividness of the arm extension illusion, and high scores tended to go along with shorter illusion latencies. This result is compatible with the view that healthy subjects’ susceptibility to experimentally induced alterations in bodily awareness may serve as a marker for their proneness to occasionally experience distortions of body schema in everyday life. The present study suggests that the body schema distortions regarded as ‘‘core perceptual aberrations’’ by the creators of the PA scale (Chapman et al., 1978) can be reflected in an individual’s responsiveness to an illusion with a known physiological basis. Alternatively, one could argue that participants high on PA were simply more suggestible than those low on PA and complied more readily with the instructions. We are not aware, however, of any published accounts of an association between PA and suggestibility.

The gender effect observed in the Pinocchio illusion deserves some comment. Here, PA was clearly associated with both extent and vividness of the illusion for the 12 men, but not for the 18 women. Vibration-induced movements activate a motor and fronto-parietal network that is clearly lateralized to the right hemisphere (Naito et al., 2005),whereas language functions are mediated rather by the left hemisphere. Neuropsychological studies have shown that men show a stronger functional hemispheric lateralization than women (Voyer, 1996). As high scores on scales measuring aberrant perceptions or thoughts are reportedly associated with a relative absence of functional hemispheric specialization (Leonhard and Brugger, 1998), we might expect men scoring high on the PA scale to have a better verbal report of their illusory experiences.

Our prediction regarding a negative association between illusion proneness and a high Need for Cognition (NFC; Cacioppo & Petty, 1982) was not borne out. On the contrary, we found indications, significant for the illusion of arm extension, for a positive relationship, with generally higher vividness ratings for participants with a high need to cognitively structure a perceptual experience. We had originally hypothesized that the more thought a participant devoted to the sensorimotor impressions connected with illusory body experiences, the more such experiences would be abolished. This prediction was based on (1) the observation that tonic activation of the vibrated muscular group is detrimental to the illusion of arm extension (Neiger et al., 1986) and (2) the fact that such activation is often a concomitant of consciously mediated motor imagery (Kitada et al., 2002). In retrospect, however, we think that a high need for consciously structuring experiences may be associated with more developed introspective abilities, which in turn allow the detection of smaller deviations from the regular size and shape of one's own body. To summarize, the present study provides some evidence for a relationship between healthy participants' susceptibility to vibration-induced phantom sensations and both their proneness to distortions of body schema in everyday life and the tendency to intellectually penetrate a sensory experience. Future studies should investigate whether these and other personality variables (see for instance MacLachlan et al., 2003) also predict the frequency and compellingness of phantom sensations in people with deafferentation syndromes. At least some of the variability in patients' phantom limb experiences may be determined by premorbid personality factors.

Study 2: Phantom Touch

There is a large body of literature on cross-modal information processing, examining how one sense influences another, including how stimulation of one sense can lead to a perception in a non-stimulated sense (e.g. how phantom sensations can be evoked by watching other people move, as in Melzack et al., 1997) and in how stimuli delivered to one sense modality interfere with stimuli delivered to another sense, even if the interfering stimuli are not attended to (e.g. Pavani, Spence, & Driver, 2000; Maravita et al., 2002). The following study investigated the interference effect of vision on touch under different viewing conditions. We examined the influence of a mirror on haptic perception. The participants were healthy volunteers and a patient with whole body deafferentation. A paper summarizing this work has been submitted to Experimental Brain Research.

Observed Touch Captures Normal and Absent Touch

Introduction

In the 18th century, George Berkeley proposed that touch was needed to educate vision. He argued that touch would give meaning to the "meaningless jumble" of retinal images (Rock and Harris, 1967) and that touch dominated vision. As early as 1937 it was shown that people are easily induced to believe that they feel what they see. Hence, vision was thought to dominate touch (Tastevin, 1937). In fact, later experiments showed that when subjects were presented with conflicting visual and haptic information (viewing a plastic square through a distorting lens and simultaneously touching it), they were more prone to believe in what they saw than what they felt (Rock and Victor, 1964). The authors concluded that vision is so "powerful in relation to touch that the very touch experience itself undergoes a change" (p. 595). This phenomenon, dubbed "visual capture of touch", seems to be such a robust effect that it has been designated as "cognitively impenetrable" (Pavani et al., 2000, p. 353). With respect to the role played by proprioceptive cues, it has been pointed out that vision has a higher reliability and spatial acuity than proprioception and that this explains why the brain would give more weight to visual information (Armel and Ramachandran, 2003). Visual capture of touch in instances of conflicting information between the visual and haptic modalities has been examined for various target features (shape or size) and with various experimental manipulations such as prism displacement and size distorting lenses (Rock and Harris, 1967). It has also been studied in different populations. Power & Graham (1976) concluded from their study with potters that the generality of the hypothesis that vision dominates touch was strengthened by their failure to refute it. Misceo, Hershberger, & Mancini (1999) studied children in three different age groups and found developmental differences in the influence of vision on touch. Vision dominated the 6-year-olds' haptic estimates, neither modality dominated in the 9-year-olds', and touch clearly dominated haptic estimates in 12-year-old children. Therefore, the authors concluded that neither touch nor vision inherently dominates perceived size. The results of Heller (1992) support this view. He used a mirror placed perpendicular to a display of tangible letters placed in front of the participants to induce a discordance between felt and seen form and direction. The majority of the subjects relied on touch perception, only one in 14 participants showed a dominance of vision. A number of subjects showed a compromise between the senses, suggesting a merging of modalities at some level of sensory integration.

It is now known that neither of the two extreme perspectives described above – touch educates vision vs. vision dominates touch – is true. With the introduction of the "optimal integration model", scientists have succeeded in determining how much weight the brain gives to signals coming from different sensory systems to arrive at plausible (and usually correct) decisions about limb position (van Beers et al., 2002). Thus, the currently held opinion is that humans rely on the sense which in a given situation yields the most information. Ernst & Banks (2002, p. 429) concluded that "visual dominance occurs when the variance associated with visual estimation is lower than that associated with haptic estimation".

In the present study we investigated the influence of vision on touch under various viewing conditions. Specifically, we studied the influence of a mirror on haptic perception. Participants had to explore the shape of two wooden objects, one with each hand, and provide same/different judgments. In some conditions direct observation of one of the exploring hands including the object was allowed. In other conditions the observation was restricted to the respective mirror image. We also investigated the performance of a patient with complete loss of touch, vibration, pressure, and proprioception, patient GL (Forget and Lamarre, 1987) to find out whether visual capture of touch might exist in the absence of phenomenal experience of touch. Evidence in favor of such an implicit effect would support previous observations of "numbsense" as an equivalent of blindsight (Rossetti et al., 1995, 2001).

Materials & Method

Participants

Able-bodied subjects: 20 participants (12 women) took part in the study. Their mean age was 28.3 years (range: 19 to 49 years). None of the participants had a history of neurologic or psychiatric disease. 18 subjects were right-handed according to a 13-item handedness-questionnaire (Chapman and Chapman, 1987).

Patient GL: a 55-year old right-handed woman with permanent loss of the large sensory myelinated fibers (as confirmed by biopsy) after two episodes of sensory polyneuropathy. GL suffers from a complete loss of touch, vibration, pressure, and proprioception up to below the level of the nose. Tendon reflexes are absent in the extremities. However, she can perform complex motor tasks under visual guidance (Forget and Lamarre, 1987; for more information see http://deafferented.apinc.org).

All participants gave written informed consent before taking part in the study, which was approved by the local ethics committee.

Materials

We used a wooden box (62 cm long, 33 cm wide, 19 cm high), with two openings on each of the longer sides to allow participant and experimenter to place their arms into the box (Ramachandran and Rogers-Ramachandran, 1996, Fig. 3.2). A vertical mirror was placed in the middle of the box, and the top of the box could be removed either on the left or on the right side of the mirror. Two wooden shapes were placed into the box, one to the left and one to the right side of the mirror. The shapes were selected from two identical sets of five items each. They varied from a perfect circle (6 cm in diameter) to an ellipse (long axis: 10 cm, short axis: 2.2 cm; Tab. 3.2).

Procedure

Prior to the actual experiment, participants saw the shapes and were invited to familiarize themselves with the wooden shapes by exploring them freely for a brief interval with both hands. For the proper experiment, participants were instructed to extend the index finger of each hand, and the experimenter placed both fingers onto the outer rim of the left and the right shape, respectively. Then, participants explored both shapes by moving their index fingers along the outer rim of the shapes. Movements of the hands had to be executed in opposite directions (clockwise with the left and counter-clockwise with the right hand or vice versa). Special care was taken to ensure that both hands were moved synchronously and that the whole shape was explored rather than only a specific area (e.g. the ends of elliptical shapes). Shift of direction during the exploration was permitted and participants were allowed to vary the speed of exploration. Compliance with these instructions was controlled by the experimenter and proved to be excellent. Instructions were identical for GL except that she was allowed to touch the whole shape with her hands. Due to her sensory deficit she was not able to use exclusively her index finger and restrict its contact to the rim of the shape only.

At the beginnig of each trial the experimenter placed the participant's index fingers (GL's hands, respectively) onto the shapes, then participants were told to start the exploration. The experimenter recorded the time needed by the participant to decide vocally whether the touched shapes were identical ("same") or not ("different"). Participants had been instructed to make this decision as quickly as possible and, if they had not given a response after 30 s, were stopped from further exploration and had to provide their best guess. Moreover, after each decision participants had to rate the confidence of their decision on a 6-point scale. The scale ranged from 0 ("0% certain that response was correct") to 5 ("100% certain), with the intermediate steps 1 to 4 indicating intermediate levels of confidence (20%, 40%, 60%, and 80% certainty, respectively).

Each participant was tested in 5 different conditions: blind (i.e., no visual feedback), two direct viewing conditions (i.e., directly watching either the right or left hand), and two indirect viewing conditions (i.e., watching either the right or left hand in a mirror; see Tab. 1). The experiment started with the "blind" condition. All other conditions were presented in a pseudo-randomized order. We decided not to include the "blind" condition in the randomized series, to allow participants to familiarize themselves thoroughly with the task and to keep the other conditions uncontaminated with possible learning effects. Patient GL was subjected to a slightly modified protocol due to time constraints and to avoid fatigue. She completed the conditions "blind", the direct viewing condition "looking at the right hand", the indirect viewing condition "looking at the reflection of the right hand in the mirror", and at the end the "blind" condition was repeated ("blind II", see Tab. 3.2).

Each condition comprised 17 experimental trials, and each trial consisted of the presentation of a different combination of two identical or two different shapes. If the shapes were not identical, they differed by 1, 2, or 3 "gaps" of intermediately sized ellipses (Tab. 3.2). Every shape combination was presented once per condition. The experimental trials were mixed with up to six control trials consisting of identical shape combinations which had been encountered before in the same condition. The control trials were not subjected to statistical analysis. They were introduced to prevent participants from counting and remembering trials with identical shape combinations in the respective conditions.

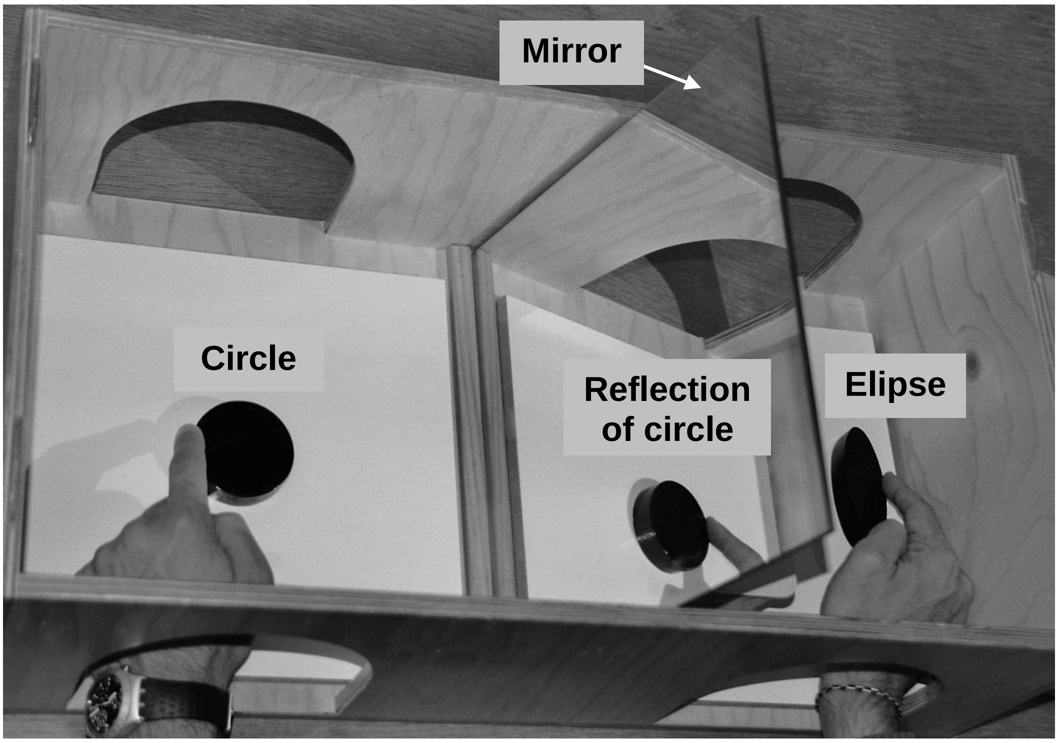


Fig. 3.2: Experimental setup showing the mirror box with a participant's hands exploring two different shapes. During the actual experiment the mirror was in place for the mirror-viewing conditions, and replaced by a non-reflective screen for the direct viewing conditions. Moreover, either half of the box or, in the blind condition, the entire box was covered. Additionally, participants were asked to remove all rings, watches or wristbands.

Results

The variables measured were reaction time (RT), number of correct responses, and confidence ratings (CR). Table 3.2 summarizes the data obtained for the able-bodied participants and for patient GL. Data were analyzed using SPSS, version 12.0.1 (SPSS Inc, Chicago, IL) and StatView, version 5.0.1 (SAS Institute, Cary, NC).

Able-bodied participants: Figure 3.3 displays the RTs in the 4 conditions and for the various gaps. We calculated two three-way ANOVAs (one for RT, one for CR) with "hand" (left vs. right), "view" (direct vs. indirect) and "gap" (0, 1, 2, 3) as factors. For the RTs we found a significant main effect for "view" ($F_{(1,19)}$= 8.1, p= .01), with participants being slower when watching the reflection of a hand compared with watching a hand directly. A significant main effect was also found for "gap" ($F_{(3,17)} = 52.5$, $p<.001$), with participants being faster the greater the gap. There were no other main effects nor interactions (all F values < 1, all p values >.549). For the CRs we only found a significant main effect for "gap" ($F_{(3,17)}= 12.8$, $p<.001$), with participants being more confident the greater the gap.

A further two-way ANOVA with the factors "view" and "hand" revealed that all participants made significantly more correct decisions, when they had a direct view of one of their hands, than when they were looking at the reflection of their hand in the mirror ($F_{(1,19)}=34.1$, $p<.001$).

Patient GL: The percentages of correct responses of the deafferented patient GL were significantly above chance level exclusively in the second "blind" condition at the end of testing. In the initial conditions "blind", "right hand" and "reflection of right hand" the performance of GL was merely at chance level, with 47%, 59% and 53% of correct responses. The confidence interval of the chance level lay between 26% and 75% of correct responses, i.e. more than 75% of the responses in any one condition had to be correct to have a performance significantly better than chance.

Non-parametric testing (Wilcoxon signed rank test) revealed that, when the correct responses alone were considered, the comparison of the RTs in the two blind conditions showed significant differences. The RTs for condition "blind II" were significantly longer than for "blind" ($Z=-2.1$, $p=.036$).

When all GL's responses were taken into consideration, irrespective of accuracy, the results resembled those of the able-bodied participants. Figure 3.4 displays the RTs in the 4 conditions, for the various gaps separately. The RTs in condition "blind" were faster than in the direct viewing condition "right hand" ($Z=-2.3$, $p=.022$) and in the indirect viewing condition "reflection of right hand" ($Z=-3.2$, $p=.001$). They were also faster than in condition "blind II" ($Z=-2.6$, $p=.009$). Moreover, the RTs in condition direct viewing "right hand" were faster than in "reflection of right hand" ($Z=-2.5$, $p=.01$). We also found the RTs for correct decision to be numerically faster than for the incorrect decisions in most conditions. Only in the direct viewing condition "right hand" this effect was significant (Mann-Whitney-$U=11.0$, $p=.019$). In the "blind II" condition, the only condition that produced above-chance results, this RT difference between correct and incorrect responses was not present at all. There were no systematic effects of the gap size on response accuracy or latency in any of the conditions.

GL used the confidence ratings inconsistently and not as instructed. More specifically, GL communicated after the experiment that she had sometimes used a rating of "3" when she was uncertain whether she had actually touched the forms, although "3" was supposed to mean "I am 60% sure that my response was right". Thus, her CRs were not subjected to statistical analysis.

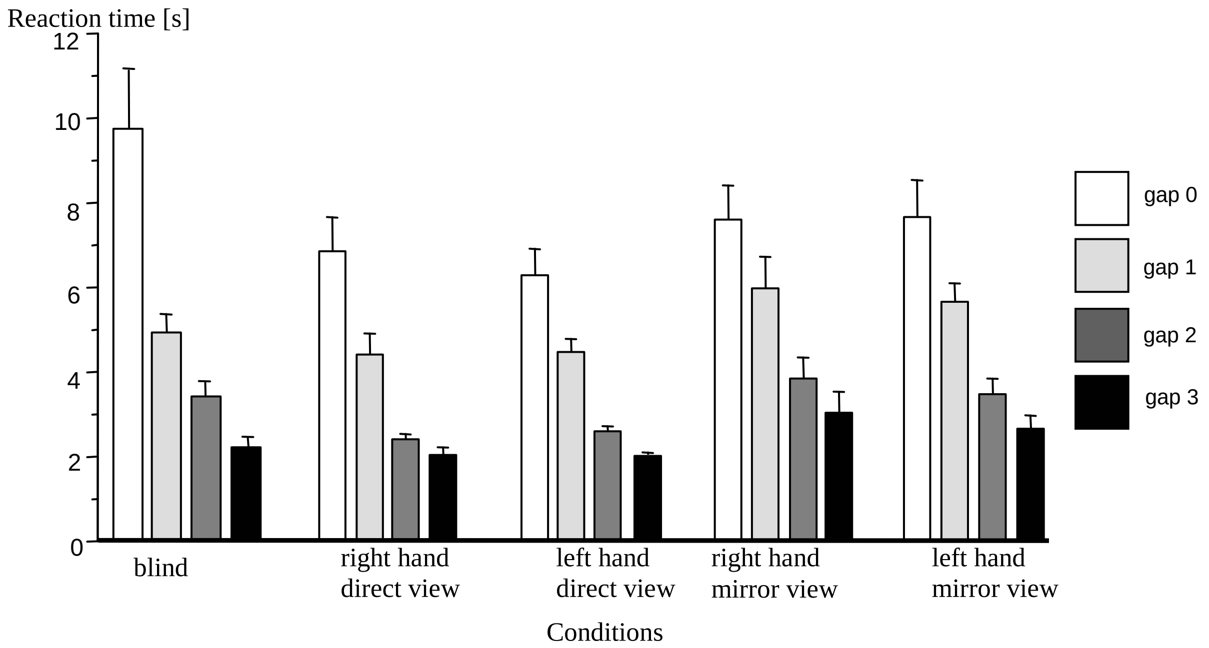


Fig. 3.3: Reaction time data for the 20 able-bodied participants in the five test conditions as a function of the difference between the two shapes ("gap").

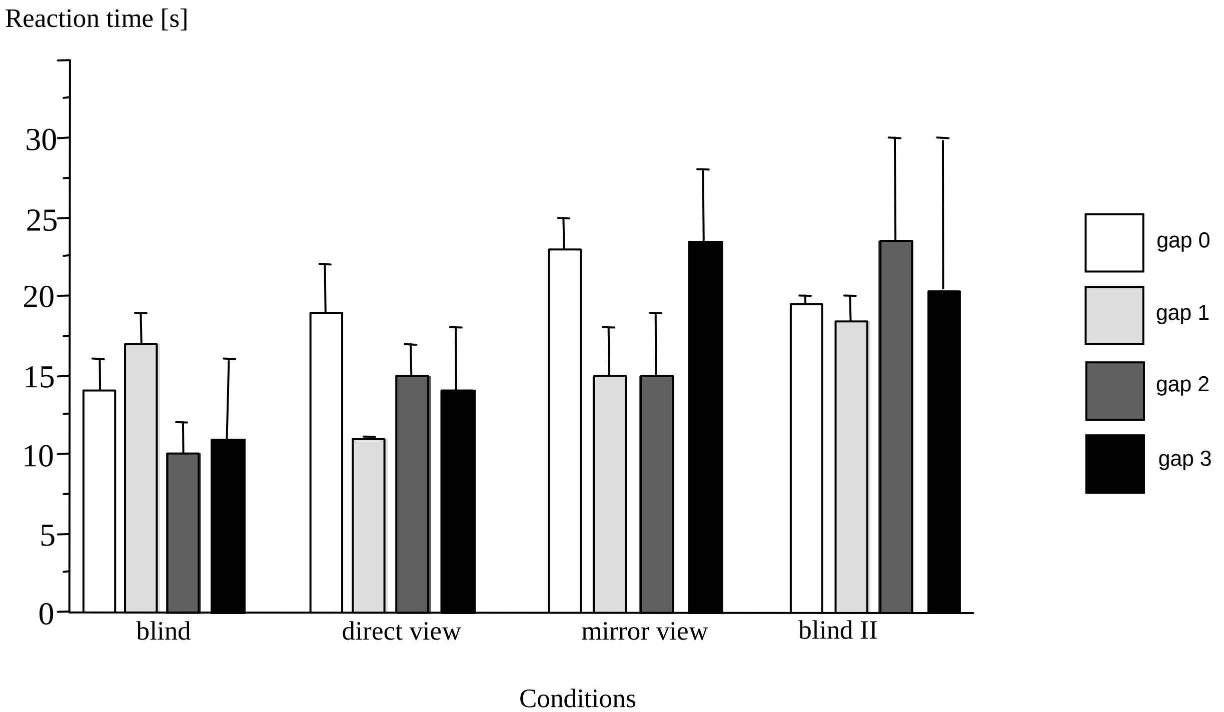


Fig. 3.4: Reaction time data for GL in the 4 conditions. As in Fig. 3.3, the 4 different colors represent the 4 different gaps.

Tab. 3.2: Mean reaction times (RT) and confidence ratings (CR) for the various experimental conditions and as a function of the gap between two simultaneously explored shapes (standard errors in parentheses)

	RT [sec]		CR	
Condition	able-bodied participants	GL	able-bodied participants	GL
blind	5.0 (.5)	11.5 (1.6)	4.6 (.1)	4.3 (.4)
direct view: observe right hand	3.9 (.4)	13.7 (1.1)	4.6 (.1)	4.6 (.2)
direct view: observe left hand	3.8 (.2)	n.a.	4.6 (.1)	n.a.
indirect view: observe reflection of right hand	5.1 (.6)	19.2 (1.7)	4.5 (.1)	4.3 (.2)
indirect view: observe reflection of left hand	4.8 (.4)	n.a.	4.6 (.1)	n.a.
blind II	n.a.	19.8 (1.7)	n.a.	4.3 (.3)
Gap	able-bodied participants	GL	able-bodied participants	GL
0: i.e. same shapes	7.6 (.7)	22.1 (2.1)	4.0 (.1)	3.7 (.2)
1: e.g. ● ⬯ ⬮ ⬯ ⬯	5.0 (.4)	15.3 (1.1)	4.5 (.1)	4.4 (.2)
2: e.g. ● ⬯ ⬯ ⬮ ⬯	3.1 (.2)	15.3 (1.7)	4.9 (.04)	4.7 (.3)
3: ● ⬯ ⬯ ⬯ ⬮	2.4 (.2)	15.8 (3.5)	5.0 (.03)	4.5 (.3)

n.a.: not administered

Discussion

With the help of three-dimensional wooden shapes and a mirror we studied the influence of vision on touch in 20 healthy volunteers. Participants had to explore two shapes simultaneously with the left and right hand and to decide as quickly as possible whether these shapes were same or different. We also subjected a patient with whole-body deafferentation, and thus without conscious haptic experiences, to a slightly modified procedure. Our main findings were (1) that visual capture of touch can be elicited in able-bodied volunteers with mirror-reflections and (2) that a similar effect can be observed in a deafferented patient who has no conscious apperception of touch.

The able-bodied participants made significantly more errors when looking into the mirror than when directly looking at their palpating hand or not looking at all. This demonstrates the influence of vision on touch. A decision is more prone to error when signals from different sensory systems need to be integrated than when attention is focused on one unique sensory system. This explains why the number of correct responses was higher in the "blind"-condition. Kennett and colleagues (2001) showed that participants were better at a two-point-discrimination task when they were able to look at a body part stimulated with pincers, than when vision of the stimulated body part was prevented. Looking at a body part thus seems to make it more sensitive. A similar effect may have happened in our study, although we studied cross-modal interactions in terms of *interference*, rather than facilitation. According to the optimal integration model participants gave too much weight to the signal coming from the "seen" hand, which masked the correct somatosensory signal from the unseen hand, thus making more errors in the indirect, mirror viewing than in the direct viewing condition.

Using RT measurements, we were able to show that the introduction of growing visual interference increasingly hampered the participants' ability to decide whether the two shapes were the same or different. This finding is in accordance with the original findings of Rock & Victor (1964) and can be interpreted as an effect of visual capture. The decrease in performance was more pronounced, the more difficult the decision was, i.e., when the gap size was small, the effect of visual capture was stronger. In other words, the introduction of either visual information or visual information derived through a mirror led to a conflict between the visually perceived and the proprioceptively perceived shape. The capacity of mirrors to induce visual capture has been described by Holmes et al. (2004) who showed that participants made reaching errors with their right arm when they were prevented from viewing this arm and instead saw the reflection of their left arm. The authors explained the observed reaching errors with the fact that participants actually felt their right arm to be in the position in which they saw it in the mirror. Unlike in this study, in our own investigation not only the felt position of the hand was important, but also the visual information coming from the shape itself. As we did not take any measures to hinder vision during the direct viewing and mirror viewing conditions (e.g. by dimming the light), we presume, in accordance with the optimal integration model, that the brain gave undue weight to the visual signal.

The CRs for correct responses did not differ between conditions. Thus, in spite of the greater difficulties to reach the correct decision as reflected in the longer RTs, participants were nonetheless able to draw conclusions with the same confidence in all conditions. The high confidence throughout the various conditions might have arisen because participants were either not aware of the increased difficulty introduced by the mirror, or they could fully compensate the effect of the mirror by taking more time to make their final decision. At the start of their first mirror condition, many participants spontaneously volunteered the information that the mirror was disturbing and making it hard for them to decide. Thus, the first explanation can be rejected. Instead, the data rather demonstrate that the participants were fully able to compensate for the mirror effect by taking more time to decide.

We wondered whether the effects seen in the able-bodied participants might also occur in the absence of touch and proprioception. Hence, we recorded data on accuracy, latency, and subjective confidence in patient GL. Her accuracy proved rather poor. In three of the four conditions she completed, her accuracy was at chance level. However, during the fourth condition (blind II), a repetition of the first condition, her accuracy level rose to over 80%. This marked rise in correct responses was accompanied by an equal slowing in RTs, which we believe indicates a change in strategy rather than an effect of fatigue. When taking into account not only the correct but all responses of GL, her RTs showed a pattern similar to that obtained in the healthy volunteers, revealing that her reactions slowed down with increasing levels of visual interference. Thus, in the haptic exploration task described here, visual interference can impede the speed of judgements about the shape of two forms being explored simultaneously with both hands, even in the total absence of touch and kinesthetic feedback from the hands.

Several mechanisms have been proposed that may explain this apparently unconscious mediation of haptic sensibility. (1) GL has intact motor fibers. It has been suggested that she uses a "central memory of motor orders" to perform proprioceptive tasks, such as to match the force produced with one hand with her other hand (Lafargue et al., 2003). Recently, in healthy subjects, Gandevia et al. (2006) reversibly anesthetized and paralysed one arm by ischemia. The subjects lost all sensations and, unbeknown to them, also all voluntary movements of the wrist, and they developed the subjective experience of a phantom hand. They were then asked to perform flexion and extension movements of the wrist, which resulted in perceived position changes of up to 20 degrees and more, although the wrist had not moved at all. From this, the authors concluded that motor outflow alone was used to signal hand position. Similarly, GL might have used information from motor commands during the exploration of the shapes to derive some unconscious information about them. (2) GL still has sensory fibers of small diameter that may forward sensory information she is able to use, albeit in an unconscious manner. As GL told us after the experiment, she used the temperature information coming from the two materials she was touching (wooden objects on coated magnetic plate) to determine whether she was actually touching the shapes. During the fourth condition ("blind II") she might have developed so much expertise in this that she was actually able to use this information to determine shape. However, this alone does not explain the effect of visual interference or visual capture reported here. Another sensory channel forwarding this effect may be some sensory receptors in the hairy skin of the hand dorsum. In humans, the hairy skin of the forearm has a dual tactile innervation consisting of fast-conduction myelinated fibers (which are absent in GL) and slow-conducting unmyelinated C-mechanoreceptive fibers, which may code innocuous skin deformation (Vallbo et al., 1993). These low-threshold C-tactile afferents have an exquisite sensitivity to light touch and can strongly respond to slow stroking of the skin with a brush (Vallbo et al., 1999). The functional property of the C-tactile fibers is still unknown and their perception may be conditional on activity in the myelinated fibers. A recent study in healthy subjects and patient GL has shed some light on this question (Olausson et al., 2002). This investigation showed that GL could detect light touch applied to the hairy skin of forearm and dorsum of the hand. She perceived the brush-evoked sensation much weaker than healthy subjects and reported them as faint and diffuse, but clearly pleasant. In contrast to the controls, the functional magnetic resonance imaging did not show any activation in primary and secondary somatosensory cortex, but mainly in the insular region. This seems to exclude some discriminative properties in this C-tactile system. However, we cannot exclude that these receptors in the hairy skin on the hand dorsum might have been activated by movements of the skin during the exploration of the shapes and thus have given rise to some perception that GL could use unconsciously. (3) Various cases of cortical deafferentation have suggested the existence of some type of "blind touch", analogous to "blindsight" (as described by Weiskrantz and Warrington, 1975). Paillard (1999) described patient RS who lost joint position sense, thermal, and pain sensations after an occlusion of the left posterior parietal artery. RS was unable to detect static tactile stimulation on her right lower arm and hand, but nevertheless was able to point accurately to the stimulated point on her affected hand with her intact hand. This ability called "blind touch" was interpreted as dissociation between the ability to localize a touch stimulus and the tactile sensory detection itself. More recently, Rossetti et al. (2001) described patient JA who suffered from a left sided parietal and thalamic lesion and, as a result, presented a complete sensory loss on the right half of the body. Unlike in GL, sensitivity to temperature was likewise abolished. Nonetheless, the patient was able to correctly point to a stimulus applied to his numb arm, despite his continuous affirmation that he did not feel anything. In analogy to blindsight, this phenomenon has been termed “numbsense”. Although JA is cortically deafferented whereas GL is suffering from peripheral deafferentation, she might exhibit numbsense as well. Interestingly, JA’s ability to identify stimuli applied to his numb arm by pointing was disrupted when he was required to respond verbally. Rossetti at al. (2001) concluded from this observation that the activation of the verbal system disrupts the numbsense. In our study GL was required to make verbal responses for stating her confidence ratings. Thus, her sensory accuracy might have also suffered from being forced to use a response modality that may have hindered her numbsense. In conclusion, it can be said that watching a mirror reflection of one's own hand is sufficient to capture touch experiences in able-bodied participants as well as in a peripherally deafferented subject and that this effect manifests itself in the accuracy as well as the reaction time data.

Study 3: *Mitempfindung* and Synesthesia

In this study a little known phenomenon called *Mitempfindung* was examined. Similarities and dissimilarities between *Mitempfindung* in synesthetes and non-synesthetes are discussed. The study will be published in a special edition on synesthesia in Cortex: Burrack, A., Knoch, D., & Brugger, P. (2006). *Mitempfindung* in Synesthetes: Co-incidence or meaningful association? *Cortex*, 42, 151-154.

Mitempfindung in Synesthetes: Co-Incidence or Meaningful Association?

Introduction

Synesthesia manifests itself in a vast variety of cross-modal associations. Despite this heterogeneity at the phenomenological level, there is general agreement about a common cause, at the neuronal and perhaps the genetic level, of the sensory referral from one modality to another. In support of the notion of a "synesthetic constitution" is the observation that most synesthetes report more than one type of synesthesia. While one of the most common forms is the association between two visual submodalities, i.e. grapheme-color synesthesia, the cutaneous senses are among the least frequently involved modalities. However, an early study described the merging of thermal and tactile impressions, the latter simultaneously being felt at a location far away from the stimulation point (Dallenbach, 1926). Specifically, this author described that coldness applied to a young woman's forearm made her aware of pressure sensations in the teeth, cheeks and other parts of her head. Dallenbach (1926) emphasized that the young woman's mother reported more traditional types of synesthesia (involving the visual, auditory, olfactory and gustatory, but not the somatosensory modality) and proposed an inherited "peculiarity of nervous structure" (Dallenbach, 1926, p. 575) common to both his subjects. Apparently unbeknownst to the author, the phenomenon of cutaneous double sensations had been described almost 200 years earlier (Hales, 1733) and was later labeled *Mitempfindung* (Müller, 1837, after the German "sensing together"), a term subsequently used also in the English language literature (e.g., Evans, 1976; Hammond and Ebers, 1992; Martin, 1991; Schott, 1988 for review). Given the above-mentioned co-occurrence of different types of synesthesia in one individual, we investigated whether the incidence of *Mitempfindung* would be higher in people with digit-color synesthesia compared to non-synesthetic control subjects.

Method

Twenty digit-color synesthetes (17 women) and 20 non-synesthetes (matched for age, gender and education) were recruited for an ongoing project in synesthesia. History of psychiatric and neurological disease was checked with an abbreviated neuropsychiatric inventory (Campbell, 2000); one of the synesthetes reported epileptic seizures, another one reported a history of unexplained fainting-attacks. All synesthetes became aware of their synesthesia in early childhood. Automaticity of individual digit-color associations was established with a random generation paradigm (Knoch et al., 2005). Synesthetes had to name (eyes closed) the colors they associated with the digits 1 to 6 in a sequence as random as possible (66 responses generated at a rate of approx. 1 Hz). Control subjects learned the 6 digit-color associations of their pair-matched synesthete and performed the same random color generation task. Synesthetes, but not controls, “counted in colors”, that is, consecutive color responses represented digits adjacent to each other on the number line.

Synesthetes were recruited by flyers and ads in a local newspaper. Matched non-synesthetic subjects were recruited among acquaintances and people attending a local recreational area. Thirty-four non-synesthetes (20 women), participating in an unrelated study, were also interviewed regarding their experience with *Mitempfindung*. All participants gave written informed consent according to the Declaration of Helsinki.

Subjects were asked whether tactile stimulation of one part of the body simultaneously produced a sensation at a different location. If the response was affirmative, the subject was asked to indicate the trigger and reference zones on a full body figure, seen from 4 different views (Richter, 1977). Moreover, subjects were required to fill in a brief questionnaire about various quantitative and qualitative aspects of their *Mitempfindung*.

Results

Mitempfindung was reported by 8 of the 20 synesthetes (7 of whom were women) and 2 of the 20 matched control subjects (both women) (χ^2 = 4.8, p < .03). Three of the 34 non-matched control subjects (two women) reported *Mitempfindung* (χ^2 = 7.5, p <.01). Most subjects indicated that they first noted the occurrence of *Mitempfindung* during early childhood or puberty. A majority of subjects reported a strictly ipsilateral referral of sensation, but no laterality differences were evident in the distribution of trigger or reference areas. The reference zones were usually located rostral to the trigger zones. For further information on the 13 subjects with *Mitempfindung* see Table 3.3.

Table 3.3

Characteristics of Mitempfindung in the 13 Subjects Reporting the Phenomenon

Subject	Gender	Age of first awareness of *Mitempfindung*	Reference zone(s) rostral to trigger zone	Trigger zone on (side of body)	Reference zone on (side of body)
1 (S)	f	not specified	not necessarily	midline	midline
2 (S)	f	17	yes	right	midline
3 (S)	f	32-37	yes	left	left
4 (S)	m	18	yes	left	left
5 (S)	f	always been aware	yes	left	left
6 (S)	f	13	yes	midline	midline
7 (S)	f	always been aware	trigger zone: anywhere reference zone: head, shoulders, toes	not specified	not specified
8 (S)	f	4	yes	left and right	midline
9 (M-C)	f	early twenties	no	left and right	left and right (ipsilateral)
10 (M-C)	f	puberty	no	midline	midline
11 (NM-C)	f	always been aware	no	left and right	left and right (contralateral)
12 (NM-C)	m	14	yes	right	midline
13 (NM-C)	f	14	yes	left	left

S = synaesthete; M-C = matched control subject; NM-C = non-matched control subject; f = female; m = male

Discussion

The incidence of *Mitempfindung* was 40% in synesthetes , 10% in the matched control group, and 9% in the non-matched control group. This renders a meaningful association between digit-color synesthesia and *Mitempfindung* plausible and supports the notion of a conceptual similarity between the two phenomena (Dallenbach, 1926; de Fromentel, 1888). Previous reports diverge with respect to the prevalence of the phenomenon in the general population. Some are vague, mentioning that it is “observed in many people” (Bean, 1979, p. 155) or “commoner than might be supposed” (Schott, 1988, p. 1188). Among those authors who provide exact figures, these vary between 8 out of 9 subjects (Mittelmann, 1920) and 8 out of 41 (Evans, 1976). This high variability is possibly a consequence of many factors, such as preselection of participants, individual differences in subjects’ introspective abilities and different assessment methods. Not only the relatively high incidence of *Mitempfindung* in synesthetes, here empirically determined for the first time, would seem to justify a conceptualization of the phenomenon as a type of synesthesia, but in addition, there are a number of striking similarities between these two unusual forms of simultaneous double perceptions. For instance, both originate in early childhood, are highly variable between individuals, but very specific and stable within an individual. The unidirectionality principle in synesthesia (e.g., an auditory stimulus elicits a color, but looking at the color rarely ever evokes an auditory experience) is also encountered in *Mitempfindung*. Typically, stimulation at one point of the body ("trigger zone") elicits a simultaneous perception at a second point ("reference zone"), but referral does not occur in the opposite direction. For further attributes of *Mitempfindung*, also characteristic of non-cutaneous synesthetic associations, see Table 3.4. The features of *Mitempfindung* assessed in our subjects (e.g., onset and unidirectionality) were consistent with the findings listed in Table 3.4.

Table 3.4

Attributes of Mitempfindung as Described in the Literature

Attribute	Reference(s)
Onset early in life or possibly congenital	Schott, 1988; Hammond and Ebers, 1992
Often runs in families	Bean, 1979 (p. 149); Dallenbach, 1926
Unidirectionality: Stimulation of a referal point never generates sensation in the trigger zone	Evans, 1976; Schott, 1988; Monro, 1898
Association between trigger and reference zone variable across individuals, but very stable within an individual	de Fromentel, 1888; Kowalewsky, 1884; Sterling, 1973; Bean, 1979; 1981; Sinclair, 1949
Possibly underreported (until questioned, subjects with *Mitempfindung* are often not aware that they experience something special)	Dallenbach, 1926 (p. 577); Sinclair, 1949
Cases of acquired *Mitempfindung* are described	Schott, 1988; Bors, 1979; Aglioti et al., 1999; Nathan, 1956; Hammond and Ebers, 1992; Turton and Butler, 2001 (for cases of acquired synaesthesia see Armel and Ramachandran, 1999; Harrison, 2001; Steven and Blakemore, 2004)

The contemporary literature conceives of *Mitempfindung* as a "neuroanatomical and physiological puzzle" (Hammond and Ebers, 1992, p. 724). Neither peripheral factors (e.g., extensive axon branching) nor mechanisms at the spinal, subcortical or cortical levels alone can fully account for the pattern of observations. Rather, studies of acquired *Mitempfindung*, i.e., the referral of sensation after peripheral or central nervous system damage (see Table 3.4

for references), suggest that referred double sensations are a general sign of neural plasticity, irrespective of the level at which irritations or deafferentations occurred. As in the literature on the non-cutaneous synesthesias (e.g., Baron-Cohen and Harrison, 1996; Grossenbacher and Lovelace, 2001), both an aberrant neural connectivity (e.g., Aglioti et al., 1999; Sterling, 1973) and the functional release of normally inhibited pathways (Hammond and Ebers, 1992) are discussed as a potential neural correlate of *Mitempfindung*. The features of apparently spontaneous and those of acquired *Mitempfindung* are very similar in that both appear at highly variable sites inter-individually, but that individual mappings of the trigger and reference zones are highly stable. Unlike spontaneous *Mitempfindung*, however, acquired *Mitempfindung* tends to be rather transient (Schott, 1988). In fact, transient *Mitempfindung* can be elicited by experimental application of acute pain to a healthy subject's hand followed by non-noxious tactile stimulation of the ipsilateral lip (Knecht et al., 1998b). These authors found that a considerable number of volunteers subjected to this procedure reported a touch sensation not only on the lip, but simultaneously in the hand. This experimentally induced *Mitempfindung* is reminiscent of "referred sensations" in amputees that involve the referral of touch applied to normesthetic body sites to the phantom limb (Ramachandran et al., 1992a). Thus, the phenomenon of *Mitempfindung* appears highly significant with respect to understanding the of processes of reorganization and plasticity. A similar conceptual background is assumed for synesthesia, both in its "natural" (Grossenbacher and Lovelace, 2001) and acquired forms (Armel and Ramachandran, 1999; Steven and Blakemore, 2004). While Table 3.4 lists the phenomenological (and possibly conceptual) similarities between synesthesia and *Mitempfindung*, we also wish to point out one discrepancy: while the incidence of synesthesia is clearly much higher in women compared to men (e.g. Harrison, 2001), to our knowledge no comparable gender bias has ever been reported for the cutaneous referral of sensation. The present study cannot contribute to the issue of gender differences in the prevalence of *Mitempfindung* since the majority of our subjects were women.

We hope that these results will raise the awareness of scientists working in the field of synesthesia for the phenomenon of *Mitempfindung*. A deeper understanding of one of the phenomena may lead to a better understanding of the other.

Study 4: The Rubber Hand Illusion in Hand Amputees: a field for future studies

In the following section I present thoughts about a study which unfortunately could not be carried out, as we were not able to recruite an adequate subject. Nevertheless, we believe the theoretical background and assumed results are worth mentioning.

Background

As explained before, it was already shown in the 1930's that people can be led to believe that a plastic finger is part of their own body (Tastevin, 1937), a manipulation which later developed into the rubber hand illusion (Botvinick and Cohen, 1998, see pg. 30). As described on page 31, several variations of the original experiment have been conducted to study the limits of the paradigm. Moreover, imaging studies have been conducted to examine brain activation during the perception of the illusion (p. 31). Most studies employing the RHI collect data on two variables: on the rubber hand questionnaire as devised by Botvinick & Cohen (1998, see Tab. 2.1) and on proprioceptive drift (PD). This term refers to the phenomenon that the conscious position sense deteriorates when a limb is kept stationary while visual feedback of the limb is denied (Wann and Ibrahim, 1992). In connection with the RHI, proprioceptive drift is measured as a displacement of the stimulated hand towards the rubber hand.

To our knowledge, no one has ever attempted to elicit the RHI in hand amputees with phantom sensations, which might seem like a vain idea at first: how could one elicit a hand illusion in a subject without a hand? Nevertheless, we believe this is possible, due to the afore mentioned phenomenon called "referred sensations" (see p. 13). A sensation is considered referred when a suprathreshold stimulus is felt not only at the stimulation site but also at another site of the body. In hand amputees, sensations may be referred into the phantom hand from stimulation on the stump and from stimulation on the face. The latter referral is possible because the face and the hand area lie adjacent to each other on the somatosensory homunculus in the primary sensory cortex of the brain (Fig. 1.1). After a hand amputation the brain area formerly used by the hand is "empty" and is being invaded by the adjacent face area. Thus, touch delivered to the face may be referred into an upper limb phantom (Ramachandran & Hirstein, 1998, see Fig. 1.2). For the same reason touch delivered to the genitals may be referred into the phantom of lower limb amputees, as has long been known by clinicians (Henderson and Smyth, 1948).

The subject to be looked for

To conduct the study as planned, the recruitment of at least one subject with upper limb amputation at the level of the wrist or higher would be necessary. This subject would not only need to experience a vivid phantom limb, but also show reliable referred sensations from the face to the phantom hand. Moreover, the phantom hand should be experienced as occupying approximately the part of extracorporeal space the real hand would occupy: it should be experienced in a regular distal position (and not telescoped into the stump). Unfortunately, the recruitment of at least one subject fulfilling all the mentioned criteria could not be accomplished. Of 22 upper limb amputees whose phantom (and referred) sensations were carefully assessed according to the SIPS, a Structured Interview of Phantom Sensations (Brugger and Regard, 1998), only one person reported a continuous presence of phantom sensations. This person, GA, is a 50-year-old male, who lost his left arm in 1974 approximately one hand below the elbow joint in an accident with a chipper. The patient experiences continuous phantom sensations of his missing hand, which is telescoped into his stump; thus, GA is not experiencing his lower left arm, only the *hand* is vividly felt. The hand is not felt to be attached to but rather to be inside his stump. His thumb, index and middle fingers are experienced as one unit, whereas the ring finger and pinky can be moved individually. Weak phantom limb pain ("electric sensation") can be provoked by manipulating the stump but apart from this, the patient does not experience phantom limb pain. GA experiences reliable and strong referred sensations from his ipsilateral cheek into his phantom hand, especially into his phantom pinky. Referred sensations are present when GA is touching his face himself, when his face is being touched by others, and during everyday activities like shaving.

GA wears a cosmetic prosthesis on a regular basis. The prosthesis does not influence the telescoped position of his hand. When the prosthesis is not worn, spontaneous movements of the hand are experienced.

Although GA experiences vivid and reliable referred sensations from tactile stimulations of the face into the phantom (Fig. 3.5), he did not fulfill the criterion of an "externalized" phantom, i.e. he experienced his phantom hand as occupying the space of his own upper stump (Fig. 3.5, right).

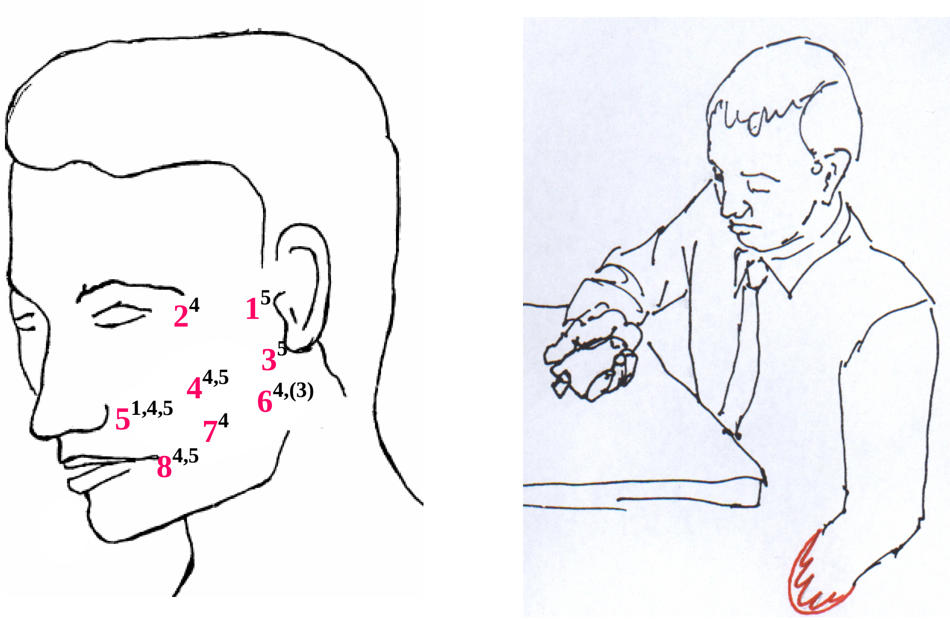


Fig. 3.5:
Left side: pink numbers: stimulation site on cheek ipsilateral to amputation; black superscript numbers: finger(s) into which stimulation was referred on three trials, whereby 1 denotes the thumb.
Right side: experience of phantom hand inside the stump as drawn by GA.

Procedure to be applied

Along with the ideal participant yet to be identified, we would like to investigate normal-limbed control subjects. Each participant will be tested in 11 consecutive conditions, which will be presented in pseudo-randomized order (see Table 3.5). Participants will be seated at a table, one hand on the table. The hand will be placed under a small wooden cover to prevent vision of the hand. Moreover, participants will wear a cloak covering their shoulders, arms and upper body to give as little visual information of the stimulated arm as possible (see Fig. 2.4). The stimulated hand will rest on a pad – only visible to the experimenter - which is covered with marks denoting distances of 1 centimeter. Outside of the participant's visual control, the index finger of the participant will be placed on top of one of the marks by the experimenter at the beginning of each condition. Care will be taken to ensure that the hand is kept in a relaxed position and as still as possible throughout every stimulation period. In each condition the hand will be stimulated for four minutes, during which participants will concentrate on the rubber hand (or in some conditions on the table surface, see Table 3.5). In one condition we will stimulate the cheek of the participant instead of the hand, in order to be able to compare the results of this stimulation with the results of the cheek stimulation in the amputee. After each minute, participants will close their eyes and point with their un-stimulated index finger to the perceived position of the stimulated index finger three times.

The difference between actual and perceived position (to the nearest centimeter) will be recorded by the experimenter. Additionally, after the fourth minute, participants will remove their hand and fill out a translated version of the questionnaire devised by Botvinick & Cohen (1998; Tab. 2.1) to rate their experiences during the completed condition.

Expected pattern of results

As described in the "background" section, data on the rubber hand questionnaire and also on proprioceptive drift should be collected. The expected results are summarized in Tab. 3.5. We expect that a condition in which no RH is present and in which there is no stimulation will not lead to an experience of the RHI (as operationalized by self report in the questionnaire data) and will only lead to a small amount of PD. This condition will thus serve as a baseline condition. Even the introduction of a RH into the experimental setup and stimulation of the RH should yield similar results. No difference is expected between the able-bodied participants and the amputee. In the illusion condition, in which the RH and the real hand are stroked in synchrony, a strong PD and a convincing perception of RHI is expected. Stimulation of the amputee's hand on his intact body side should yield results comparable to those of the able-bodied participants. During asynchronous stimulation of the RH and the real hand, we expect a PD and a RHI experience that lies in between the results of the illusion condition and the three conditions described first, in which only little PD and no RHI is expected. Again, stimulation of the amputee's hand on his intact body side should yield results comparable to those of the able-bodied participants. When the cheek and the RH are stimulated we expect a deviation of results between able-bodied participants and amputee(s). The former are not expected to experience a RHI, likewise they are not expected to show a PD significantly greater than in the control condition. The amputee(s), on the other hand, should show a RHI and a PD that are comparable with the illusion condition and which are significantly stronger than those of the able-bodied participants in this condition.

To conclude, we strongly believe that the elicitation of the RHI is possible in adequate participants, however difficult it might be to find them. We believe that the phenomenon of referral of touch and, more importantly, of attributes of the self, by tactile stimulation of the face deserves to be studied. This variant of the RHI would illustrate the primacy of cortical distance over that of contiguity of stimulus application.

Tab. 3.5: Conditions to be applied in the study.

Condition	Stimulation on Body	Rubber Hand Stimulation	Expected Effect on PD and Perception of RHI
1 – no stimulation/RH absent 1.a) on dominant side 1.b) on non-dominant side	no stimulation	no RH present, gaze directed towards table, no stimulation,	- some proprioceptive drift (Baseline) - no RHI
2 – no stimulation/RH present 2.a) on dominant side 2.b) on non-dominant side	no stimulation	gaze directed towards RH, no stimulation	- proprioceptive drift comparable to Cond. 1 - no RHI
3 – no stimulation/RH stimulation 3.a) on dominant side 3.b) on non-dominant side	no stimulation	yes	- proprioceptive drift comparable to Cond. 1 - no RHI
4 – illusion condition 4.a) on dominant side 4.b) on non-dominant side	hand	yes	- strong proprioceptive drift - strong RHI
5 – asynchronous condition 5.a) on dominant side 5.b) on non-dominant side	hand	yes	- proprioceptive drift greater than in Cond. 1 - weak RHI
6 – cheek/RH	- *able-bodied participants*: cheek of dominant side - *amputee*: cheek of amputation side	yes	- *able-bodied participants*: proprioceptive drift comparable to Cond. 1, no experience of RHI - *amputee*: strong proprioceptive drift, experience of RHI

Condition 1: Participants are seated in the appropriate position, no RH is present. Participants are required to focus on the table next to their hidden hand; no stimulation is applied to the hand. This condition serves as a baseline condition for the amount of PD that could be expected without manipulation. Condition 2: As in 1, this time the RH is present and the participants are asked to focus on it. Again, there is no stimulation. Condition 3: As in 2, stimulation is applied to the RH only. Condition 4: Synchronous stimulation of RH and real hand. In this condition a strong effect on PD and experience of the RHI are expected. Condition 5: The stimulation of RH and real hand are not synchronized in time. A weak effect on PD and experience of the illusion are expected. Condition 6: As in 4, but instead of stimulating the real hand, the cheek is stimulated. A noticeable effect on PD and perception of RHI are only expected for the hand amputee. Conditions are presented in a pseudo-randomized order. All participants are given all conditions, amputees will be administered conditions 1-5 on their non-amputated side only and condition 6 on their amputated side.

Abbreviations: PD = proprioceptive drift; RH = rubber hand; RHI = rubber hand illusion

Chapter 4

General Discussion

The aim of the present thesis was to better understand the body representation of able-bodied persons by manipulating their corporeal awareness. Through the examination of healthy subjects and a patient with disturbed corporeal awareness it was possible to gain insight into when, why, and to what extent the body representation can be altered experimentally. The studies introduced in this thesis addressed this main question as to when and why the brain produces illusory corporeal experiences from different perspectives. They will now be discussed in turn.

I investigated the issue of **individual differences in the perception of bodily illusions** in healthy subjects with the help of two vibration-induced phantom illusions: illusory arm extension and nose prolongation (‘‘Pinocchio illusion’’). Susceptibility to the illusions was quantified by vividness ratings and by ratings of the amount of illusory position changes of the arm and illusory shape changes of the nose. Participants also completed the Perceptual Aberration (PA) questionnaire, which reflects the frequency of spontaneously experienced body schema alterations and the Need for Cognition (NFC) inventory, which measures a person’s tendency to cognitively structure experiences. PA was positively correlated with participants’ susceptibility to illusory arm extension and, exclusively for men, also to nose elongation. A high NFC was weakly associated with a high susceptibility for the Pinocchio illusion. These findings illustrate a cognitive mediation of experimentally induced phantom sensations and revealed that our brain is rather reluctant to let us experience changes in bodily perception. It takes some practice to learn how to elicit the illusion reliably and even then it is only experienced by a small percentage of people subjected to the procedure. There might be a threshold up to which the brain manages to "buffer" the illusory perception, and if the threshold is crossed, the perception suddenly flips and the illusion is perceived. This might also explain why the subjects who did experience the illusion did not doubt its existence. The extent of the illusion varied between subjects, but no subject who did feel the illusion doubted afterwards that they had actually experienced it. Moreover, the data indicate that the experience of the Pinocchio-Illusion is to some extent influenced by gender and personality factors. This has not been previously noted in the literature on phantom sensations, but a comparable modulation is known in higher order disturbances of body perception, e.g. in OBEs. Up to at least 1935 it was even argued that almost exclusively women would experience these and similar reduplicative phenomena of their own body (Menninger-Lerchenthal, 1935), a notion that has by now been discounted (Bradford, 2005).

To elicit what may be referred to as **"phantom touch"**, I used a simple mirror device in 20 able-bodied participants and in a patient (GL) with deafferentation from the level of the nose downwards. The experimental set up allowed the investigation of cross-modal interference effects between seeing and feeling. All participants had to provide same/different judgments regarding bi-manually explored wooden shapes under various viewing conditions. The mirror condition produced reliable interference effects on response accuracy and latency in both healthy participants and patient GL. This is interpreted as "visual capture of touch" induced by a mirror and indicates, in the case of GL, the presence of "numbsense", a form of residual tactile sensitivity equivalent to blindsight in cortically blind patients. Thus, touch can be "captured" by visual observation, even though the touch experience is not consciously perceived. The effect of visual capture proved to be quite strong, manifesting itself in each of the examined subjects. It is therefore argueable that this effect is more robust and thus not as easily influenced by personality variables as is the Pinocchio-Illusion.

Visuo-tactile enhancement has repeatedly been examined in healthy subjects, but has also been noted in the clinical environment. Rorden and colleagues, in an extension of a report by Halligan et al. (Halligan et al., 1996), showed improved tactile sensitivity in a patient with an impaired tactile sense in the frame of a neglect syndrome. The authors showed that a visual stimulus applied at the same time as and in the vicinity of a tactile stimulus increased the number of perceived tactile stimuli significantly (Rorden et al., 1999). They argued that this improved performance could not simply be attributed to the fact that the proximity of the stimuli enhanced perception, but to the fact that both the visual and tactile stimulus were attributed to the same limb. The authors suggested that high-level visual information can modulate tactile perception. Specifically, it is known from work with monkeys (Graziano et al., 2000) and humans (di Pellegrino et al., 1997) that peripersonal space is represented in a multisensory way. It is against this background that a "mirror therapy" of phantom pain in arm amputees has been developed (Ramachandran et al., 1995) and is applied in hemiplegic patients to improve sensorimotor functions by movement observation (Altschuler et al., 1999). With regard to cross-modal visual-somatosensory integration in amputees, it has long been known that a phantom percept can be elicited by watching other people moving their limbs (Brugger et al., 2000). Here, the concept of mirror neurons may be relevant (Rizzolatti and Craighero, 2004), perhaps especially so in people who are missing limbs from birth (Melzack et al., 1997).

A phenomenon known from healthy volunteers but also from amputees was to be examined in the study about ***Mitempfindung***. *Mitempfindung* is the referral of a tactile sensation to a location far away from the stimulation site (see Schott, 1988, for a review). The incidence of *Mitempfindung* in the normal population is not clear, indications lie between 8 out of 9 (Mittelmann, 1920), 8 out of 41 (Evans, 1976), and 3 out of 34 subjects (Burrack, Knoch, & Brugger, in press). An equivalent double-percept occurs in some amputees and is called "referred sensation". While early studies suggested a narrow somatotopic organization of referred sensations (Ramachandran and Hirstein, 1998), later studies were more cautious and admitted that they can be elicited not only from, say, face to hand, but also from a variety of body sites with no apparent proximity on the level of cortical representation areas (Knecht et al., 1998a). This brings the phenomenon of referred sensations phenomenologically even closer to the phenomenon of *Mitempfindung*, as a clear somatotopy is also lacking in the case of the latter (e.g., see Tab. 3.3). Originally, my contribution to the issue of *Mitempfindung* was planned as a neuroimaging approach, possibly elucidating the neural correlates of this "mysterious form of referred sensation" (Richter, 1977, p. 4702). Unfortunately, I was not able to proceed along these lines, as the phenomenon was encountered in fewer people than we had expected. In the few volunteers who reported reliable *Mitempfindung*, the trigger zones were located in a way that made it impractical to study them in the fMRI environment (e.g. trigger zone located on the back, inside the ear canal or on taboo zones). For that reason I began studying *Mitempfindung* in healthy subjects who are experiencing some sensory stimuli in a very special way, i.e. digit-color synesthetes. Synesthesia comes from the Greek *syn* = together and *aisthesis* = perception and denotes the involuntary experience of a cross-modal association. That means, in synesthetes the stimulation of one sensory modality also causes a perception in one or more other sensory modality (Cytowic, 1995). Most synesthetes experience more than one type of synesthesia which let to the concept of a "synesthetic constitution". While synesthesia is most often associated with the visual sense (as in digit-color synesthesia), the cutaneous senses have also been noted as a source of synesthetic experiences. Given the mentioned synesthetic constitution I was interested to examine whether the incidence of *Mitempfindung* would be higher in people with digit-color synesthesia compared to non-synesthetic control subjects. I found a significantly higher incidence of *Mitempfindung* in synesthetes compared to a control group of non-synesthetes, and my review of the literature revealed a surprising number of similarities between *Mitempfindung* and other known forms of synesthesia. This does not answer the question if

Mitempfindung and referred sensations share a common neurophysiological background, but it does support the notion that there is a conceptual similarity between the two phenomena.

A planned study on **phantom touch in an amputee** could not be conducted as I was not able to find the required research subject(s). I failed to find the extremely special subject fulfilling all inclusion criteria, i.e. (1) amputation of upper limb, (2) vivid and continuous phantom hand sensations, (3) phantom sensations must not be painful, (4) reliable referred sensation from face to hand, and (5) phantom hand occupies extracorporeal space (i.e., is not telescoped into stump). I found one highly cooperative participant, who fullfilled criteria 1 to 4, but not criterion 5. This study thus still awaits realization.

To sum up, the studies of this thesis show how surprisingly easy the perception of the human body may be altered, how easily even perceptions which are not even consciously experienced may be manipulated and how far the interconnections between phenomena that had not been previously considered to be connected go. On the other hand this thesis also shows, how large the individual differences in our bodily perceptions are and thus how important they are to be considered in every explanation regarding corporeal awarness and its manipulations.

Future Research and Open Questions

While trying to find answers to the question of when and why the brain may produce illusory corporeal experiences, a number of new and more concrete questions arose, which deserve further study and consideration. Among them are…

- …whether it is possible to make a direct connection between the results obtained in able-bodied subjects and the phenomena patients experience. Here the Pinocchi-study offers a good opportunity, by showing that personality variables influence the way the illusion is experienced. It leaves open, however, the question whether personality variables form a predisposition for experiencing non-experimental phantom sensations, i.e. the experience of phantoms after deafferentation and/or de-efferentation, and in cases of congenital limb absence.

- …whether the higher incidence of *Mitempfindung* found in synesthetes compared to non-synesthetes is mirrored, within a population of amputees, in a higher incidence among those with as compared to those without referred sensations. If this were the case, a central nervous system mediation common to both phenomena of *Mitempfindung* and referred sensations would appear even more probable. As noted in the closing sentence of the paper version of the respective study: "A deeper understanding of one of the phenomena may lead to a better understanding of the other".

- ...whether it is possible to find at least one subject with reliable *Mitempfindung* which could then be studied with psychophysical paradigms or in a neuroimaging approach to uncover more about its underlying mechanisms.

- ...whether there is a connection between *Mitempfindung* and the experience of the rubber hand illusion and the susceptibility to interactions between vision and touch. Concretely, are subjects with a history of *Mitempfindung* more prone to experience the rubber hand illusion than those without? Would they evidence higher interference effects in the mirror paradigm adopted in study 2?

- ...whether a change in the response mode would have rendered GL's (the deafferented patient's) performance in the mirror box experiment radically different. Concretely, would she have shown a greater accuracy in determining whether the shapes she was touching were same or different if the response modality had not been verbal? Rossetti and colleagues described another deafferented patient, JA, who was able to point to a stimulus applied to his deafferented hemibody, but was not able to localize that same stimulus verbally. The authors concluded that the activation of the verbal system disrupted the "numbsense" sensations found in their patient (Rossetti et al., 2001). Further study with GL is needed to determine if the same holds true for her.

Appendix

Materials used in Study 1

German Version of the Need for Cognition Questionnaire

Bitte beantworten Sie die folgenden Fragen auf einer Skala von "1" bis "7" wobei "1" bedeutet "trifft überhaupt gar nicht zu" und "7" bedeutet "trifft voll zu". Es gibt keine richtigen oder falschen Antworten, es geht um ihre subjektive Einschätzung.

- Wenn ich eine Aufgabe erledigt habe, die viel geistige Anstrengung erfordert hat, fühle ich mich eher erleichtert als befriedigt.
- Wenn ich mir eine Meinung zu einer Sache bilden soll, verlasse ich mich ganz auf mein Gefühl.
- Es genügt mir, einfach die Antwort zu kennen, ohne die Gründe für die Antwort auf ein Problem zu verstehen.
- Ich glaube, ich kann meinen Gefühlen vertrauen.
- Bei Kaufentscheidungen entscheide ich oft aus dem Bauch heraus.
- Ich denke, dass ich den Charakter einer Person sehr gut nach ihrer äusseren Erscheinung beurteilen kann.
- Ich versuche, Situationen vorauszuahnen und zu vermeiden, in denen die Wahrscheinlichkeit gross ist, dass ich intensiv über etwas nachdenken muss.
- Wenn es um Menschen geht, kann ich meinem unmittelbaren Gefühl vertrauen.
- Wenn die Frage ist, ob ich anderen vertrauen soll, entscheide ich normalerweise aus dem Bauch heraus.
- Ich finde es nicht sonderlich aufregend, neue Denkweisen zu lernen.
- Mein erster Eindruck von anderen ist fast immer zutreffend.
- Ich akzeptiere die meisten Dinge lieber so wie sie sind, anstatt sie zu hinterfragen.
- Denken entspricht nicht dem, was ich unter Spass verstehe.
- Die Vorstellung, mich auf mein Denkvermögen zu verlassen, um es zu etwas zu bringen, spricht mich nicht an.
- Ich trage nicht gern die Verantwortung für eine Situation, die sehr viel Denken erfordert.
- Ich bin ein sehr intuitiver Mensch.
- Ich vertraue meinen unmittelbaren Reaktionen auf andere.
- Ich kann mir über andere sehr schnell einen Eindruck bilden.
- Ich spüre es meistens sofort, wenn jemand lügt.
- Bei den meisten Entscheidungen ist es sinnvoll, sich auf sein Gefühl zu verlassen.
- Ich würde lieber eine Aufgabe lösen, die Intelligenz erfordert, schwierig und bedeutend ist, als eine Aufgabe, die zwar irgendwie wichtig ist, aber nicht viel Nachdenken erfordert.
- Ich finde wenig Befriedigung darin, angestrengt stundenlang nachzudenken.
- Das Denken in neuen und unbekannten Situationen fällt mir schwer.
- Ich erkenne meistens, ob eine Person Recht oder Unrecht hat, auch wenn ich nicht erklären kann, warum.
- Abstrakt zu denken reizt mich nicht.
- Es genügt, dass etwas funktioniert, mir ist egal, wie oder warum.
- Wenn ich mich (mit dem Auto/Velo) verfahren habe, entscheide ich mich an Strassenkreuzungen meist ganz spontan, in welche Richtung ich weiterfahre.
- Der erste Einfall ist oft der beste.
- Ich würde lieber etwas tun, das wenig Denken erfordert, als etwas, das mit Sicherheit meine Denkfähigkeit herausfordert.

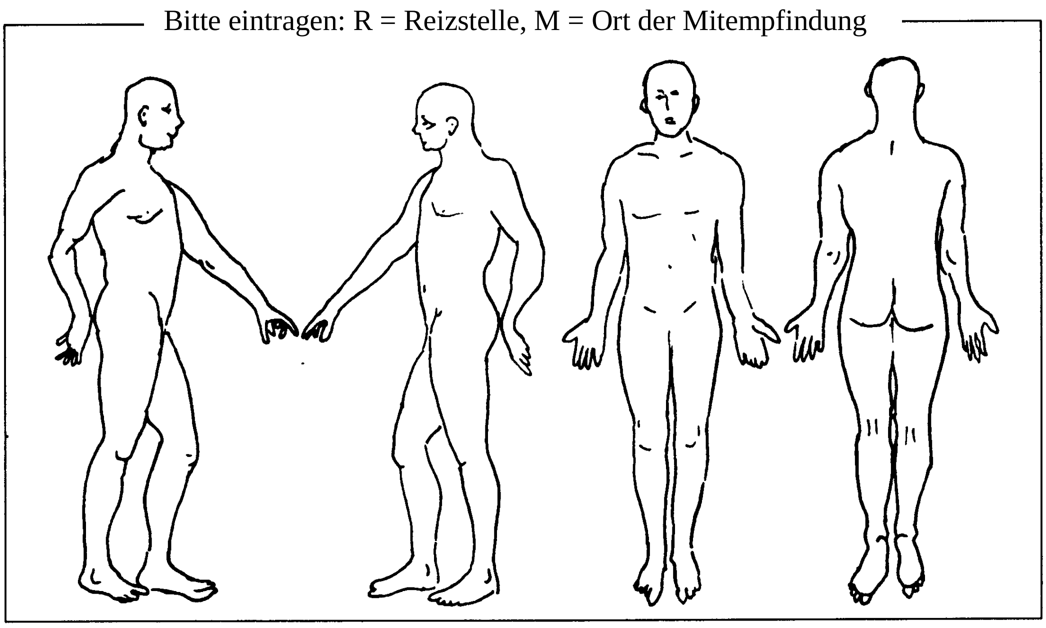
German Version of the Perceptual Aberration Questionnaire

Bitte beantworten Sie die folgenden Fragen mit "Stimmt" oder "Stimmt nicht". Es gibt keine richtigen oder falschen Antworten, es geht um ihre subjektive Einschätzung.

- Ich fühlte mich schon manchmal verunsichert darüber, ob mein Körper wirklich der meine ist.
- Ich hatte schon den Eindruck, als ob mein Kopf oder meine Beine irgendwie nicht meine eigenen sind.
- Ich hatte schon den Eindruck, als ob mein Körper sich auflösen würde.
- Manchmal muss ich mich selbst anfassen, um sicher zu sein, dass ich noch da bin.
- Ich habe schon das Gefühl gehabt, ein Arm oder Bein von mir würde nicht zu meinem restlichen Körper gehören.
- Ich habe schon das Gefühl gehabt, dass ein Teil meines Körpers grösser ist als gewöhnlich.
- Es kommt öfter vor, dass Lichtquellen in Räumen so hell sind, dass sie unangenehm für meine Augen sind.
- Manchmal, wenn ich Dinge wie Tische und Stühle anschaue, kommen sie mir fremd vor.
- Ich hatte schon den momentanen Eindruck, dass Dinge, die ich anfasse, an meinem Körper haften bleiben.
- Es gab schon Zeiten, da fragte ich mich, ob beim Körper wirklich der meine ist.
- Ich kann mich daran erinnere, dass es mir schon so vorkam, als ob eines meiner Körperglieder eine ungewöhnliche Form habe.
- Ich hatte schon das Gefühl, dass etwas von ausserhalb meines Körpers ein Teil meines Körpers ist.
- Teile meines Körpers erscheinen mir gelegentlich tot oder unwirklich.
- Ich hatte schon das Gefühl, dass Teile meines Körpers nicht zu ein und demselben gehören.
- Mein Gehör ist manchmal so empfindlich, dass mir gewöhnliche Geräusche unangenehm sind.
- Es kam schon vor, dass Teile meines Körpers kleiner als gewöhnlich zu sein schienen.
- Manchmal habe ich schon das Gefühl gehabt, mein Körper sei nicht normal.
- Manchmal habe ich schon so empfunden, als ob ich meinen Körper nicht von den Dingen um mich herum unterscheiden könnte.
- Ich hatte schon vorübergehend den Eindruck, dass mein Körper unförmig geworden ist.
- Ich habe schon das Gefühl gehabt, dass Teile meines Körpers nicht mehr zu mir gehören.
- Mein Hör- und Sehsinn war schon an mehreren Tagen hintereinander so stark ausgeprägt, dass ich mich auf nichts anderes mehr konzentrieren konnte.

Material used in Study 3

Full body figures used to record *Mitempfindung*



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Curriculum Vitae

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1989-1996:	Kurt-Schwitters-Gymnasium Misburg, Hannover, Germany.
1996-1999:	Study of Psychology at the Universität Trier, Germany.
1999-2002:	Study of Psychology at the Heinrich-Heine-Universität Düsseldorf, Germany.
2001-2002:	Diploma Thesis on "Therapy-induced cortical reorganization in stroke patients after Constraint-induced-movement-Therapy – a fMRI-Study" (in German) under supervision of Prof. Dr. W. H. R. Miltner at the Friedrich-Schiller-Universität Jena, Germany.
2003-2006:	Ph.D. Thesis on "Neuropsychological Studies of Phantom Sensations and Corporeal Awareness in Healthy Subjects" under supervision of PD Dr. Peter Brugger and Prof. Dr. Lutz Jäncke at the Universität Zürich, Switzerland.
	Ph.D. Neuroscience Program at the Zentrum für Neurowissenschaften Zürich (ZNZ) of the Universität Zürich, Switzerland.
	Clinical assistent for neuropsychological assessments and expertises at the Unit for Neuropsychology at the Clinic for Neurology of the UniversitätsSpital Zürich, Switzerland (under direction of PD Dr. P. Brugger, formerly Prof. Dr. M. Regard)
2006:	Ph.D. in Neuropsychology at the University of Zürich, Switzerland

Zürich, September 2006

List of Publications

Publications in peer reviewed Journals

Burrack, A., Hepp-Reymond, M.-C. & Brugger, P. (submitted). Observed Touch Captures Normal and Absent Touch. *Experimental Brain Research*.

Burrack, A., Knoch, D., & Brugger, P. (2006). *Mitempfindung* in Synesthetes: Co-incidence or meaningful association? *Cortex*, 42, 151-154.

Burrack, A. & Brugger, P. (2005) Individual differences in susceptibility to experimentally induced phantom sensations. *Body Image*, Vol 2/3, pp 307-313.

Conference Talks

"Toward a Science of Consciousness"-Conference, Tucson, USA, April 2004
Where Does My Nose End? Interindividual differences in susceptibility to the Pinocchio-Illusion

Ph.D.-Retreat of the Zentrum für Neurowissenschaften Zürich, 2003
Phantom illusions in healthy volunteers - the -"Pinocchio-Nose"

Poster Presentations

Autumn School in Cognitive Neuroscience, University of Oxford, UK, September 2005
News on the Pinocchio-Illusion

October-Symposium of the Zentrum für Neurowissenschaften Zürich, 2005
The Rubber Hand Illusion in Hand Amputees – What to Expect?
(selected for Datablitz presentation)

Mid-Year Meeting of the International Neuropsychological Society (INS), Dublin, Ireland, July 2005
1. The Incidence of *Mitempfindung* in Synaesthetes and non-Synaesthetes
2. Visual Capture of Touch in a Subject without Touch

October-Symposium of the Zentrum für Neurowissenschaften Zürich, 2004
Visual Capture of Touch in a Subject without Touch

Ph.D.-Retreat of the Zentrum für Neurowissenschaften Zürich, 2004

The Incidence of *Mitempfindung* in Synaesthetes & non-Synaesthetes

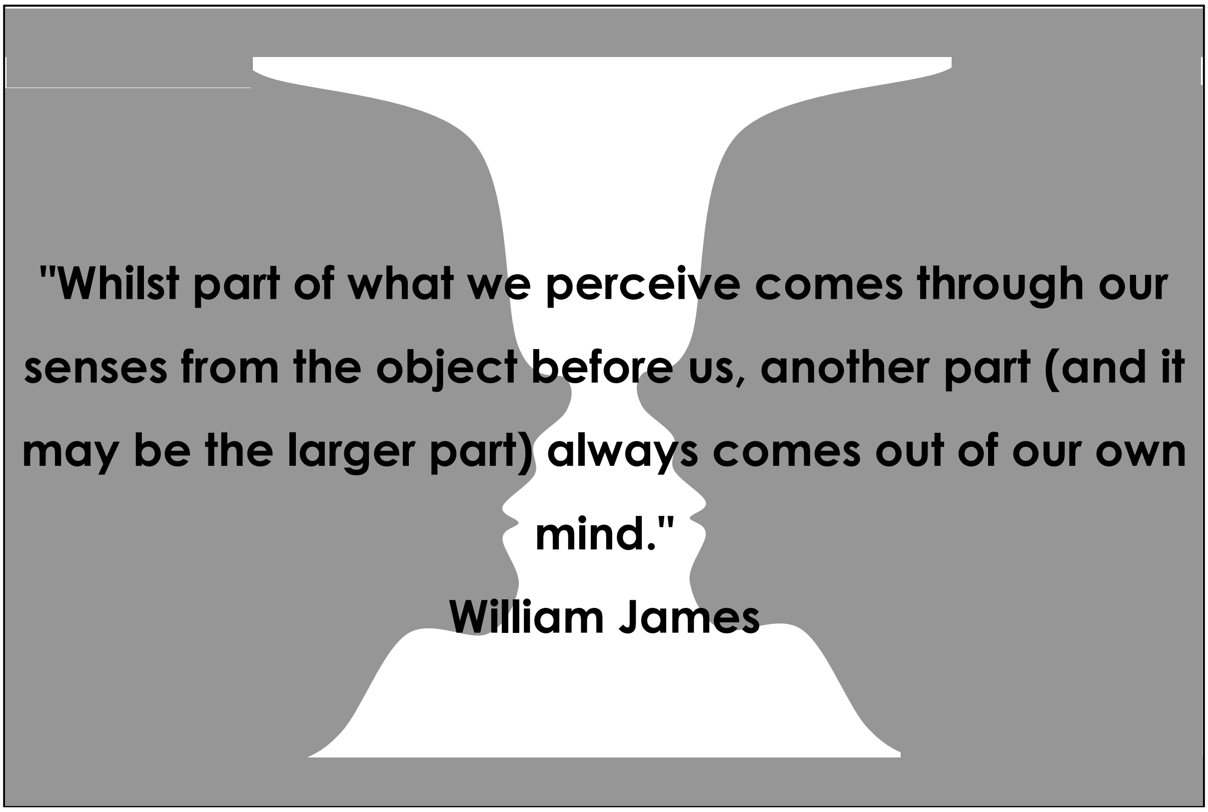
Meeting of the Swiss Society for Neuroscience (SSN), Lausanne, January 2004

"Where does my nose end?" Individual differences in the Pinocchio-Illusion

(selected for Datablitz presentation)

October-Symposium of the Zentrum für Neurowissenschaften Zürich, 2003

“Oh my gosh! My nose isn’t growing!” - Why can’t the Pinocchio-Illusion be elicited in everybody?



"Whilst part of what we perceive comes through our senses from the object before us, another part (and it may be the larger part) always comes out of our own mind."

William James